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**VARIATIONS IN BODY COMPOSITION
AND ENERGY UTILISATION BY
SOUTHERN ELEPHANT SEAL PUPS
OVER THE FIRST YEAR**

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF

THE DEGREE OF

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I, Martin Biuw, hereby certify that this thesis, which is approximately 60,000 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

Date.....12/4/04.....

Signature of candidate...

I was admitted as a research student in September 1998 and as a candidate for the degree of Doctor of Philosophy in September 1999; the higher study of which this is a record was carried out at Macquarie Island and in the University of St Andrews between September 1998 and October 2003.

Date.....12/4/04.....

Signature of candidate...

I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate for the degree of Doctor of Philosophy in the University of St Andrews and that the candidate is qualified to submit this thesis in application for this degree.

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Signature of supervisor.

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This thesis is dedicated to the memory of

Giovanni Gozzo

and

Petter Danielsson

May you always travel the oceans of time on wings of memory

INTRODUCTION

The main objective of this thesis has been to expand on previous studies of variations in maternal expenditure in phocids in general and southern elephant seals in particular, by focusing not on expenditure itself, but rather on the consequences of this expenditure for the offspring. Our approach was to measure in detail the changes in body composition (and not only body mass) of individual pups throughout their first year from reaching nutritional independence. The motivation for this objective will be discussed below, and can briefly be summarised as follows:

The extreme sexual dimorphism and more than threefold range in maternal mass in elephant seals would suggest that their lifetime fitness is very much size and/or condition dependent, and they have consequently received considerable attention over the past 3-4 decades as one appropriate model species for studying the evolution and ecological significance of maternal care. Although the basic underlying theories has general support in the scientific literature on elephant seals, the relationships between the condition of a mother and her expenditure on offspring are less apparent than we might expect. We know that larger females produce larger pups, and the range in pup mass at birth and weaning are extreme. However, relative expenditure appears to be reduced among larger mothers, and it is not clear what the variability in weaning mass consists of in terms of somatic size and energy reserves. Are there systematic differences in body composition between large and small pups, or is there some optimal body composition that maximises an individual's chances of survival? If such an "ideal fatness" exists, is it constant among individuals, or does it depend on overall size, gender and/or other unknown individual characteristics? In short: how important

is fat compared to protein for the performance and survival of elephant seal pups over the intermediate term, and how important is this early performance on subsequent performance and long-term reproductive fitness?

The structure of this thesis is slightly different from conventional theses submitted to universities in the United Kingdom. This is in part because some of the work presented has already been published in a peer-reviewed journal (Biuw et al., 2003), and because other components are close to submission in the form of manuscripts. As a consequence, all data analysis chapters have been written in the form of manuscripts, and there is no dedicated chapter presenting the materials and methods used. This introduction was written with the intention of providing the main theoretical background to the work, but each data chapter contains a more specific introduction related to the topic at hand. The last chapter is a brief summary of the main findings. It discusses the results in relation to some of the ideas put forth in this general introduction, with specific references also made to topics introduced in the main analysis chapters.

In Chapter 1, I will review the ecological underpinnings and research that has shaped our current theories on the evolution and significance of different maternal strategies in mammals. I will focus on pinnipeds, in particularly elephant seals. I will briefly describe the present status and structure of the world southern elephant seal population, highlighting the special characteristic of the Macquarie Island stock, and finally, I will give a very brief account of the physical and biological oceanography of the Southern Ocean in which these seals are an important top predator.

In Chapter 2, I will describe the individual variation and changes in body condition (size and composition) of individually marked southern elephant seal pups at Macquarie Island during the 3-8 week long fasting period after they have been abandoned by their mothers. I will describe the general functional relationships, and compare the results with previous work conducted on northern elephant seals at Año Nuevo, California, and southern elephant seals, mainly at South Georgia and King George Island. I will also describe and quantify the distribution of the variation around these general relationships, since this variation is often the more interesting, if understated, ecological aspect. Lastly, I will extrapolate on these results in an attempt to build a conceptual model of the changes in body composition during the ~1-month long transit period to distant foraging grounds after pups have departed. Although not presented in detail in this thesis, I will draw on the extensive satellite telemetry data available from a sub-sample of these seals. Based on these data, I will try to estimate the relative importance of lipid and protein as fuel stores, and speculate on the likely probability and cause of mortality during this continued fast at sea.

In Chapter 3, I will develop and a biomechanical model for estimating the relative body composition of seals while at sea, using simple dive characteristics obtained using satellite telemetry from the same sub-sample of pups and an additional number of seals from an earlier deployment. I will evaluate the accuracy of the model using computer simulation, and make some first predictions of changes in relative body composition of pups throughout the first trip to sea. This work has recently been published (see references in the chapters below), and was used to construct the conceptual model in Chapter 1.

In Chapter 4, I describe the variation and changes in mass and body composition of (mostly) the same individually marked pups during their first and/or second trips to sea. Again, I will describe the general functional relationships between these changes as well as attempt to describe the variation around these relationships. I will also examine how body mass and condition influences the haulout patterns and first-year survival probabilities, and discuss the implications in terms of how these early characteristics may affect the subsequent survival and, indirectly, reproductive success of offspring.

Finally, Chapter 5 will be a very brief summary of the main results of the three separate studies, and I will attempt to relate it back to the underlying theories and main hypotheses described in Chapter 1.

The work presented here is unique for a marine mammal. It is the first time we have been able to follow individual offspring throughout their first year of life, and to measure the changes in mass and body composition occurring during this critical period. This was made possible by the nature of Macquarie Island, and by the extensive field support provided there by the Australian Antarctic Division. As will be shown below, Macquarie Island is a very isolated island in the Western Pacific sector of the Southern Ocean, and seals returning for their haulouts are very unlikely to utilise other islands in the region. Furthermore, Macquarie Island is rather small in size (~34 x 5 km), and this allowed us to search the entire coastline on a regular basis for returning seals. We therefore had a unique ability to recapture any of our study animals when they returned for their winter and/or moulting haulouts, and the dataset

presented here is extremely rich and will provide important insights into elephant seal biology and pinnipeds biology in general for many years to come.

CHAPTER 1: ECOLOGICAL THEORY AND BACKGROUND

The fate of a population of organisms is ultimately determined by two fundamental factors, both of which act directly on the individuals within it. These are: 1) The probability of an individual surviving to reproductive age, and 2) the number of *viable* offspring produced during an individual's reproductive life. In this context, the word *viable* plays a crucial role, because it implies a continuous "feed-forward" mechanism between these two factors. The number of viable offspring produced is naturally a function of the probability of the individual offspring surviving until they become reproductively active. In order to understand how these two fundamental factors influence the dynamics of a population, we need to understand how individuals respond to various types of stochastic and systematic variations of both extrinsic (environmental/physical) and intrinsic (biological/ within-species) origin. This can only be achieved through detailed and long-term studies of known individuals.

Longitudinal studies of the reproductive performance of known individuals are commonplace in the literature, resulting from extensive research on organisms representing most animal taxa. In the case of large and long-lived vertebrates, longitudinal studies require long-term commitment from researchers and funding bodies. Long time-series, involving several generations of known individuals, are consequently rare among large mammalian species, with a few notable exceptions. Our current understanding of the links between individual reproductive success and population dynamics of large mammals comes from studies of mainly terrestrial

species such as ungulates (Albon and Clutton-Brock, 1988; Albon et al., 2000; Clutton-Brock et al., 1992; Coulson et al., 2001; Festa-Bianchet et al., 1998; Jorgenson et al., 1993; Kruuk et al., 1999; Moss, 2001), primates (Ha et al., 2000; Nishida et al., 2003; Sauther et al., 1999) and big felines (Marker et al., 2003; Packer et al., 1988; Smith and McDougal, 1991).

For obvious reasons, similar studies have been more problematic in the case of marine mammals. These animals spend all or a large fraction of their time in the water, and direct observation of complex behaviours and measurements of growth and energetics are not possible for many of these species. This problem is especially severe among cetaceans (whales, dolphins and porpoises), dugongs and manatees that spend their entire lives in the water, but also impedes the detailed study of the reproductive behaviour of walrus and some seal species that breed on unstable habitats such as pack ice. There are, however, some important exceptions. In all otariids (sea lions and fur seals) and some species of phocids (“true” seals), adult females return to land during a more or less constricted time period to give birth and nurse their pups. Adult males are also present during these periods, since the large female aggregations presents an opportunity for multiple matings and thus the potential for high reproductive output. The relative scarcity of suitable ground for these breeding aggregations, and the regularity with which seals return to them, have provided scientists with excellent opportunities to monitor known individuals over several years and breeding events. The most comprehensive of these studies to date have focussed on Northern fur seals (*Callorhinus ursinus*) (Gentry, 1999), Antarctic fur seals (*Arctocephalus gazella*) (Boyd et al., 1995; Lunn et al., 1994), Northern elephant seals (*Mirounga angustirostris*) (Crocker et al., 2001; Le Boeuf and Reiter,

1988), Southern elephant seals (*M. leonina*) (Arnbom et al., 1997; Fedak et al., 1996; Galimberti and Boitani, 1999; McCann et al., 1989; McMahon et al., 2000a, 2003) and grey seals (*Halichoerus grypus*) (Fedak and Anderson, 1982; Pomeroy et al., 1999). These studies have been used as examples of the very different parental strategies of otariids vs. phocids, and have vastly increased our understanding of male and female reproductive behaviour, sexual selection theory and, in many cases, the way in which these are influenced by foraging behaviour and environmental variation. These results have been comprehensively reviewed by Trillmich (1996), and will be briefly outlined in the following sections.

Long-term studies like those mentioned above have resulted in significant advances in our understanding of reproductive behaviour and energetics and, in some cases, how these are affected by variations in foraging success. Many studies have also described the effects of maternal expenditure on changes in body size and/or condition of pups during lactation and in some cases during the post-weaning fast on land. Furthermore a few studies have also been able to describe the effects of reproductive expenditure on the future reproductive success of females (see for instance Boyd et al., 1995 and Pomeroy et al., 1999). However no studies have yet described the potential benefit of maternal expenditure in terms of the survival and recruitment of offspring into the breeding population. Such information is crucial if we are to fully understand the causes and consequences of reproductive expenditure on the dynamics of populations.

Parental expenditure & investment

Parental care is energetically expensive. In mammals, gestation and lactation requires the input of large amounts of material and energy from the mother, both for producing

and rearing young as well as for her own maintenance. Moreover, a variety of behaviours associated with reproduction, such as territorial defence, mating and offspring guarding can also incur high costs for males as well as females. Pinnipeds have proven to be excellent subjects for studies of parental investment and reproductive success, mainly because of their relatively high reproductive costs, exclusive maternal care, spatial and temporal separation between feeding and lactating, and also because of their wide range of breeding systems and sexual dimorphism (Trillmich, 1996, see also below).

The evolution of parental care will depend on a trade-off between the costs of care to the parent's future fitness (or residual reproductive value) and the benefits in terms of the fitness of offspring or other relatives (Trivers, 1972). (Clutton-Brock and Godfray, 1991) distinguishes between three fundamental measures of parental care:

Parental care: Any form of parental behaviour that is likely to increase the fitness of the offspring, for instance food provisioning and vigilance,

Parental expenditure: The expenditure of parental resources such as energy (including metabolic overheads) and time,

Parental investment: The extent to which parental care on individual offspring reduces the parent's residual reproductive value, i.e. the sum of all future reproductions.

Limiting this discussion to large long-lived mammals, several studies on many species under various conditions have measured parental expenditure as energetic cost (Anderson and Fedak, 1985; Arnbom, 1994; Clutton-Brock, 1988; Clutton-Brock et al., 1983; Fedak and Anderson, 1982; Festa-Bianchet et al., 1996; Festa-Bianchet et

al., 1995; Keech et al., 2000; Le Boeuf et al., 1989; Le Boeuf and Reiter, 1988). Some studies have also measured the investment in terms of the fitness cost on future reproduction of the parent (Arnbom et al., 1997; Boyd et al., 1995; Clutton-Brock et al., 1983; Gaillard et al., 2000; Kruuk et al., 2000; Le Boeuf and Reiter, 1988; Lunn et al., 1994; Pomeroy et al., 1999). Only a few studies have quantified the return on this investment in terms of the survival of offspring, and in most of these studies, this return was measured as offspring survival and/or growth until fledging or weaning (Arnbom et al., 1993; Birgersson and Ekvall, 1997; Bowen et al., 2001; Fedak et al., 1996; Gaillard et al., 2000; Keech et al., 2000). However, parental investment can also have important effects on post-weaning survival and future reproductive success of the offspring. The best data on these longer-term relationships probably comes from studies on ungulates. For instance, Côté and Festa-Bianchet (2001) showed that first-year survival in mountain goat (*Oreamnus americanus*) kids can be related to kid weaning mass, which in turn is related to the mass of their mothers, and Albon and Clutton-Brock (1988) showed that the mass of Red deer (*Cervus elaphus*) calves at birth is an important determinant not only of their own adult size, but also the size and lifetime reproductive success of their calves.

The data on long-term links between maternal investment and offspring survival and growth is much less complete for marine mammals. Some recent studies have tried to fill this gap. In otariids, Baker and Fowler (1992) found that survival of northern fur seal pups to age two was related to weaning mass in males, but not on females, while Bradshaw et al. (2003) did not find any significant mass effects on early (47-day) survival of New Zealand fur seal (*Arctocephalus forsteri*) pups. In phocids, McMahon et al. (2003) showed that the weaning mass of southern elephant seal pups influenced

their survival, mainly over the first year of life. However, neither of these studies explicitly examined how these survival estimates were affected by maternal size or energy expenditure prior to lactation. Moreover, no studies on marine mammals have yet been able to measure the effects of maternal expenditure or offspring birth mass on the future reproductive success of the offspring.

Sex ratio and resource allocation

Over the decades since Fisher (1930) first published his theories about the allocation of parental resources into sons and daughters, many studies have been carried out to test these hypotheses. Assuming a parent has a finite amount of resources available, his theory states that these should be divided equally between all offspring. However, if one sex is more costly to produce, Fisher (1930) argued that the sex ratio (or energy allocation ratio) should be biased towards the less costly sex. More recently, Trivers and Willard (1973) suggested that in polygynous mammals, a female in better than average condition should allocate a greater proportion of her resources into male offspring, and Maynard Smith (1980) expanded these ideas, proposing that parents should allocate more into the sex that shows the greatest increase in future reproductive output in response to this investment. According to these ideas, in polygynous and sexually dimorphic mammals, a mother capable of producing a good quality offspring would have more grand-offspring if she bears a son, whereas if she can only produce a poor quality offspring, she should produce a daughter. According to theory, we should expect either the ratio of males to females born to increase with increasing female quality, and/or that mothers should expend more energy on male offspring after birth.

Researchers testing these hypotheses have generally looked for evidence in the form of 1) unequal sex ratio at birth, 2) unequal offspring mass at birth and/or weaning, or 3) growth and metabolic rate of pups during lactation (reviewed in Trillmich, 1996). While some studies have found differences consistent with theory (e.g. Anderson and Fedak, 1987; Bérubé et al., 1996; Birgersson, 1998; Braza et al., 2000; Kohlmann, 1999; Lee and Moss, 1986; Wolff, 1988), others have not (e.g. Campagna et al., 1992; Derocher and Stirling, 1998; Kretzmann et al., 1993; Laurenson, 1995; Smiseth and Lorentsen, 1995). Data from the red deer study on Rhum may explain some of these inconsistencies. In this species, male mating success is about three times more variable than that of females, and while a cow will produce at most one calf per year, a successful stag can sire several dozens of calves each year while an unsuccessful stag may never father any calves at all. This extreme pattern, along with the long-term research effort and impressive level of detail, have made it possible to examine the degree to which sex ratio and energy allocation are affected by different factors, such as environmental variation, population density and individual parental characteristics. For instance, the number of male calves born decreases as a function of increasing rainfall during pregnancy as well as with increasing population density, while it increases with the mother's dominance (Kruuk et al., 1999). Depending on the complexity of these types of interactions, any simple correlations between maternal expenditure and the fate of offspring in relation to sex may either accentuate or cancel each other out, leading to the notorious inconsistencies observed between other studies.

Pinnipeds display the most extreme range of sexual size dimorphism of any mammalian taxa. This variation is strongly related to the type of mating system

(Alexander et al., 1979), and this remains true after controlling for phylogenetic relatedness between species with similar degrees of sexual dimorphism (Lindenfors et al., 2002). Early on, researchers therefore recognised pinnipeds as excellent subjects for studies of differential allocation into male and female offspring. The most dramatic size dimorphism is found among polygynous, land-breeding species such as otariids, elephant seals and some populations of grey seals, and we should therefore expect similar relationships among these species as those found in terrestrial polygynous species such as deer. For instance, among northern elephant seal males, dominance and copulatory success are positively related to body mass (Haley et al., 1994), and dominant southern elephant seal bulls may be responsible for up to 98 % of all observed copulations (Bester and Wilkinson, 1994). Although these observational estimates of male reproductive success do not always agree entirely with results from genetic paternity tests (Hoelzel et al., 1999), there seems to be little doubt that the high degree of variation in lifetime reproductive success of males is fairly closely correlated with body mass and/or condition (Le Boeuf and Reiter, 1988). We might therefore expect the birth sex ratio or differential maternal expenditure between male and female pups to vary with for instance maternal quality in a similar way as has been observed in red deer. However, the evidence in support of differential expenditure or unequal sex ratio among polygynous pinnipeds is inconclusive (reviewed by Trillmich, 1996). In short, it appears well established that in otariids, male pups are born heavier and grow faster than female pups, but that maternal expenditure (measured as milk transfer) does not differ significantly (see Trillmich (1996) and references therein). It appears likely that this pattern is a result of male pups being heavier and growing faster, while females are smaller but accumulate relatively more energy (stored as lipid), as has been demonstrated in

Antarctic fur seals (Arnould et al., 1996). In phocids, the pattern is slightly less clear. While some studies on grey seals have shown that larger mothers are more likely to produce male pups (Anderson and Fedak, 1987), and that male pups are born heavier, have higher growth rates and are heavier at weaning (Kovacs and Lavigne, 1986), others have found no such differences (Bowen et al., 1992; Pomeroy et al., 1999).

As shown by the following discussion based on studies on from elephant seals, the inconsistencies among results from studies on pinnipeds may depend to some degree on the methods of analysis. McCann et al. (1989) and Campagna et al. (1992) found no differences in mass at birth and weaning or growth rate of southern elephant seal pups over lactation, and similarly, Kretzmann et al. (1993) found that male and female northern elephant seal pups did not differ significantly in any of the common measures of differential investment (mass at birth and weaning, milk intake, metabolic rate or growth rate). However, Kretzmann et al. (1993) did not relate their findings to any measures of maternal condition or expenditure, and Campagna et al. (1992) used a crude categorical index of mother's size in their study. In contrast, Arnobom et al. (1994) showed that at all maternal sizes, male southern elephant seal pups were significantly heavier at birth than female pups. However, they found no difference in pup weaning mass between males and females after the mother's size had been controlled for (Arnobom et al., 1993), and Fedak et al. (1996) found no evidence of differential expenditure (measured as relative mass loss) of mothers to male and female pups.

It appears that the relationship between female condition, pup sex and condition, and maternal resource allocation in pinnipeds is not a simple one. Following, Trillmich

(1996) a conceptual model where the mass (condition) of offspring varies nonlinearly or sigmoidally with maternal resources may more accurately describe these relationships (Figure 1).

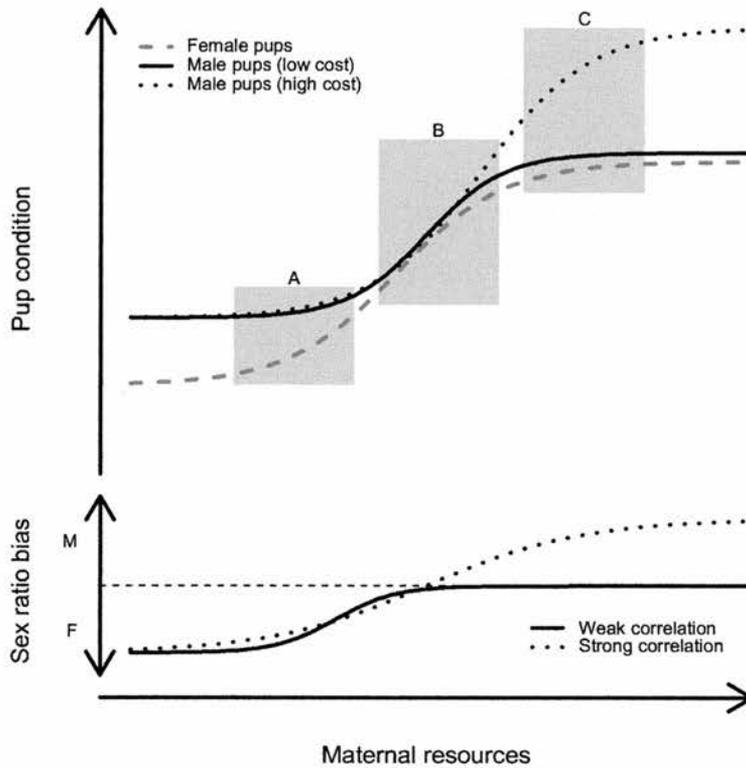


Figure 1. Conceptual representation of hypothetical relationships between maternal resources, pup body condition, pup sex and sex ratio in polygynous pinnipeds (based on ideas summarised in Trillmich (1996). Shaded areas illustrate possible confounding effects of restricting the range over which relationships are examined. A) Basic size (energetic requirement) of male pups is greater. Since they are limited by the maximum possible resource transfer of mothers, their condition does not increase significantly with increasing maternal resources, while the condition of female pups increases. B) No restrictions, and pup condition increases with maternal resources for both sexes. C) Two alternatives: strong (dotted line) or weak (solid line) correlation between male pup size and the marginal fitness benefits (i.e. higher reproductive success of male offspring) to females in good condition. The two curves of sex ratio bias also represent different strengths of this correlation. In reality, Southern elephant seal mothers with low resources produce few or no male offspring (Arnbom et al. ,1994), resulting in the solid sex ratio curve. This also suggests that the solid black curve representing male pup condition is truncated at the lefthand side (low maternal condition) because of the excessively high cost to the low-resource females of producing male offspring.

As an example, we can interpret the results from southern elephant seals using this conceptual model. Arnborn et al. (1994) found a clearly non-linear relationship between maternal post-partum mass (MPPM) and birth sex ratio. Small females (less than ~ 400 kg) produced only daughters, but above that threshold size, the ratio rapidly increased to roughly equal (compare solid line at the bottom of Figure 1 above). In terms of differential expenditure, this appeared to be limited to the period prior to birth. Birth mass was the only feature of maternal expenditure that varied between the sexes, and the relative difference in birth mass between males and females was greatest among pups born by small females (Arnborn et al., 1994) (compare solid line at the top in Figure 1 above). Post-partum expenditure of a mother (relative to her stored resources) was not significantly different between male and female pups (Arnborn et al., 1997), and the relative amount that mothers expend on their pups showed little consistent trend with the mother's size (Fedak et al., 1996). Instead, while small mothers are only able to produce small pups at a relatively high cost, some large mothers can produce large pups at only moderate expenditures. However, there appears to be an upper limit on the resources expended by large mothers, and this limit is not determined by the mother's size. The largest mothers therefore utilize relatively less of their stored resources instead of producing extremely large pups (Fedak et al., 1996).

The patterns observed in southern elephant seals therefore appears to be most accurately described by the solid black lines in Figure 1 above. One likely explanation for this may be outlined as follows:

Male pups are more costly to bring to parturition. Selective abortion or increased mortality of male foetuses results in a paucity of males born by females below a

certain size threshold, and the average birth mass of male pups is therefore higher than for female pups.

There is a strong correlation between pup condition and first-year survival up to a certain threshold. Above this threshold, the correlation disappears, and future survival is affected less by early body condition and more by subsequent behaviour and physiological development.

The large variance in reproductive success of adult males is mostly a result of different growth trajectories during the subadult years, and is not closely related to early body condition or maternal expenditure. The marginal fitness return to larger mothers for increasing their expenditure diminishes, and their lifetime fitness is most likely improved by reducing their relative expenditure to increase their own future reproductive success.

It is important to emphasize that the discussion above may not only apply to the variation in fitness benefit caused by variations in reproductive success of male offspring. In capital breeders such as elephant seals and some grey seals, there appears to be a substantial degree of individual variability in the lifetime reproductive success of females (Pomeroy et al., 1999), and the functional relationships between maternal condition and offspring success, regardless of their sex, may not be as different as previously suggested. Nevertheless, the above interpretation highlights the importance of studying reproductive strategies within a framework of environmental variation and offspring development after reaching independence. For example, the second point above was highlighted by Trillmich (1996), who pointed out that in species where males undergo a dramatic growth spurt during the subadult years (such

as elephant seals), food availability at the time of this growth spurt will be more important for adult size than the size at birth or weaning.

In summary, the selective pressure on mothers to invest more in sons than in daughters may therefore be weaker than previously assumed. Moreover, variations in for instance resource (prey) abundance may influence the cost-benefit function differently, depending on whether it selectively affects mothers before parturition, pups after weaning, or if both are affected. Only through detailed study of all these components can we hope to fully understand the links between the costs of parental expenditure and the fitness return in terms of the future reproductive success of mothers as well as their offspring.

Physiological ecology

Because seasonal fasting and foraging cycles play such a central role in the life history of phocids in general and elephant seals in particular, it is likely that the ability of young seals to adjust their patterns of energy acquisition and expenditure in response to current and potential future physiological demands will have a strong influence on their probability of survival and, ultimately, their lifetime fitness.

Theoretical and predictive models have been developed in order to understand the dynamics of fitness maximisation, especially in species experiencing seasonal and/or unpredictable food resources. The underlying assumption of these “Optimal Body Mass” models (OBM, Lima, 1986) or “adaptive fat models” is the existence of a trade-off between the costs and benefits of large energy (fat) stores. While the benefits of large energy stores are fairly obvious (i.e. energy reserves for periods of low food

availability, and thermal insulation), the costs are less easily defined. They can include for instance increased risk of predation due to reduced agility and/or reduced vigilance while actively feeding, and increased costs of locomotion due to drag and body mass. Models of this type have been used to describe the costs and benefits of varying degrees of winter fattening in birds (e.g. Houston and McNamara, 1993; Lima, 1986). As an example, when resources are predictable, the benefits of extensive fattening are reduced or eliminated, while the costs remain the same (Lima, 1986; Rogers, 1987).

In many species there is also a trade-off between energy allocation into somatic growth and energy storage (e.g. Rogers and Heath-Coss, 2003). This is likely to be especially important in species that live in seasonal environments and/or that display strong seasonality in their patterns of resource acquisition and expenditure. The dramatic seasonal pattern of fasting on land and foraging at sea displayed by land-breeding phocids is an obvious example. This trade-off may also vary with age and sex. For instance, energy allocation to reproduction has a high priority in individuals that have reached sexual maturity, and the trade-off should therefore be skewed towards energy storage, while pre-reproductive individuals of younger age classes may direct more energy into somatic growth (e.g. Post and Parkinson, 2001; Rogers and Smith, 1993). Males and females from sexually dimorphic species are likely to have very different life history strategies, and interactions between sex and age will likely result in very different trade-offs for males and females. For instance, while most female southern elephant seals give birth for the first time around age 4 (McCann et al., 1979; McMahon et al., 2003), at a body mass of ~300 – 400 kg (Boyd et al., 1994), males do not generally become reproductively active until around 8-9

years of age (Laws, 1953; McCann, 1985) at a body mass of ~ 1800 – 2000 kg (Boyd et al., 1994), and the reproductive success of male elephant seals is strongly positively related to body mass (Bester and Wilkinson, 1994; Le Boeuf, 1974). At 3-4 years of age, females should therefore switch to a strategy favouring energy storage rather than somatic growth, while male seals should favour somatic growth until at least ~ 9-10 years of age in order to increase their reproductive fitness.

While differences in reproductive strategies between adult male and female phocids have been shown to affect their seasonal patterns of energy storage and expenditure (e.g. Beck et al., 2003), differences in resource allocation may occur during their first years of life as sexual dimorphism begins to manifest itself. In pinnipeds, there is some evidence that male and female pups allocate the resources obtained through suckling in slightly different ways. For instance, Antarctic fur seal pups consume similar amounts of milk during lactation regardless of sex, but male pups direct more of this consumption into somatic growth while female pups accumulate greater lipid energy stores, and male pups are consequently heavier but leaner at weaning, while female pups are lighter but have proportionately more body lipid (Arnould et al., 1996). Similar results have recently been reported for northern fur seals (Donohue et al., 2002), and for Subantarctic fur seals (*Arctocephalus tropicalis*) by Beauplet et al. (2003), who also reported that male pups rely to a higher degree on lipid as metabolic fuel during the post-weaning fast compared with female pups. In contrast to these findings in otariids, no such differences have been reported for lactating phocid pups (Kretzmann et al., 1993). The most efficient way for phocid pups to take onboard the large amounts of milk energy during the very short lactation period is by assimilating these resources into their lipid stores rather than convert it to protein tissue. While it is

possible that sexual differences in the re-distribution of body stores similar to those demonstrated for fur seal pups may occur later, for instance during the post-weaning fast, no studies to date have found any evidence of this (Carlini et al., 2001; Noren et al., 2003).

These relationships may be further complicated by the fact that the “optimal” trade-off between energy storage and somatic growth for an individual of a given age and sex may also be influenced by a variety of intrinsic and extrinsic factors. As has been shown by OBM models and adaptive fat models in birds and fish (see references above), changes in body composition may affect the biomechanics of movements. The increase in body size due to lipid accumulation may increase the resistance force caused by body drag, while the amount of muscle tissue available to counteract this resistance remains constant. The accompanying reduction in agility is likely to increase the foraging costs and may also make animals more exposed to predation (see below). One component that may appear on both sides of this cost-benefit equation is body density. The buoyancy of a seal is largely determined by the relative amounts of low-density lipid tissue and high-density lean tissue (Beck et al., 2000; Biuw et al., 2003; Webb et al., 1998). It is likely that the overall energetic expenditure during a dive is minimised if the total body density is similar to that of the surrounding water. When southern elephant seal pups depart on their first trip to sea they are generally slightly positively buoyant, but as their relative lipid content decreases during the initial transit to suitable feeding grounds, they become gradually more negatively buoyant, before they again increase their relative lipid stores and become less negatively (or sometimes positively) buoyant (Biuw et al. (2003), see also Chapter 3, this volume). These changes are likely to be reflected in variations in

diving metabolic rate over time, determined mainly by the absolute deviation from neutral buoyancy. Furthermore, Post and Parkinson (2001) showed that if the risk of predation is inversely related to body size (due to for instance gape-limited piscivory), juvenile growing fish can incur a net survival advantage by adopting a somatic growth maximising strategy when mean growth rates during the feeding period are limited by prey availability, whereas an energy storing strategy incurs a net survival advantage if mean growth rates during the feeding period are high. This is because in the first instance, increased somatic growth reduces the risk of predation, while in the latter case the increased energy stores at the end of the feeding period reduces the risk of starvation during the subsequent non-feeding (winter) period. It is not known to what extent predation on juvenile pinnipeds (by for instance killer whales, *Orcinus orca*) is selective in terms of size or body condition. The greater diving ability of, for instance, larger southern elephant seal pups (Hindell et al., 1999; Irvine et al., 2000) may increase their ability to evade predation. However, the movements of individuals with a very high lipid content may be restricted by buoyancy and body drag (see above), and this could potentially increase the risk of predation.

Southern elephant seals: population status and life history

The southern elephant seal is a species of many extremes. They are the largest of all extant pinnipeds (adult males approaching 4 tonnes (Ling and Bryden, 1981)); they show the most extreme sexual size dimorphism of any mammals (males sometimes being more than ten times the size of the females with which they mate); they go through extreme seasonal fluctuations in body mass and lipid as a result of periods of fasting on land fasting at sea; they undertake extremely wide-ranging and long-lasting

foraging migrations (Hindell and McMahon, 2000; Jonker and Bester, 1998; McConnell and Fedak, 1996), and have an extraordinary diving behaviour, being capable of repeatedly diving for more than 45 minutes to depths of almost 2000 meters (Bennett et al., 2001; Hindell et al., 1991; Hindell et al., 1992); SMRU and CNRS-CEBC, unpublished data). Because of the characteristic land-breeding phocid pattern and the relative ease of handling these seals in the field, Southern elephant seals have become one of the main species for studying the causes and consequences of individual variation in reproduction and energy expenditure. Southern elephant seals breed on islands or isolated mainland coasts in the sub-Antarctic region. They undertake long at-sea migrations throughout the ACC and to the Antarctic continental shelf areas, and they are also known to haul out in smaller numbers along the Antarctic coast. They are an important top predator in the Southern Ocean ecosystem, but their diet is still poorly known. It is believed to consist mainly of squid, but interactions have been reported between seals and fisheries such as the longline fishery for Patagonian toothfish (*Dissostichus eleginoides*) (McMahon et al., 2000b and Field & Biuw, personal observation).

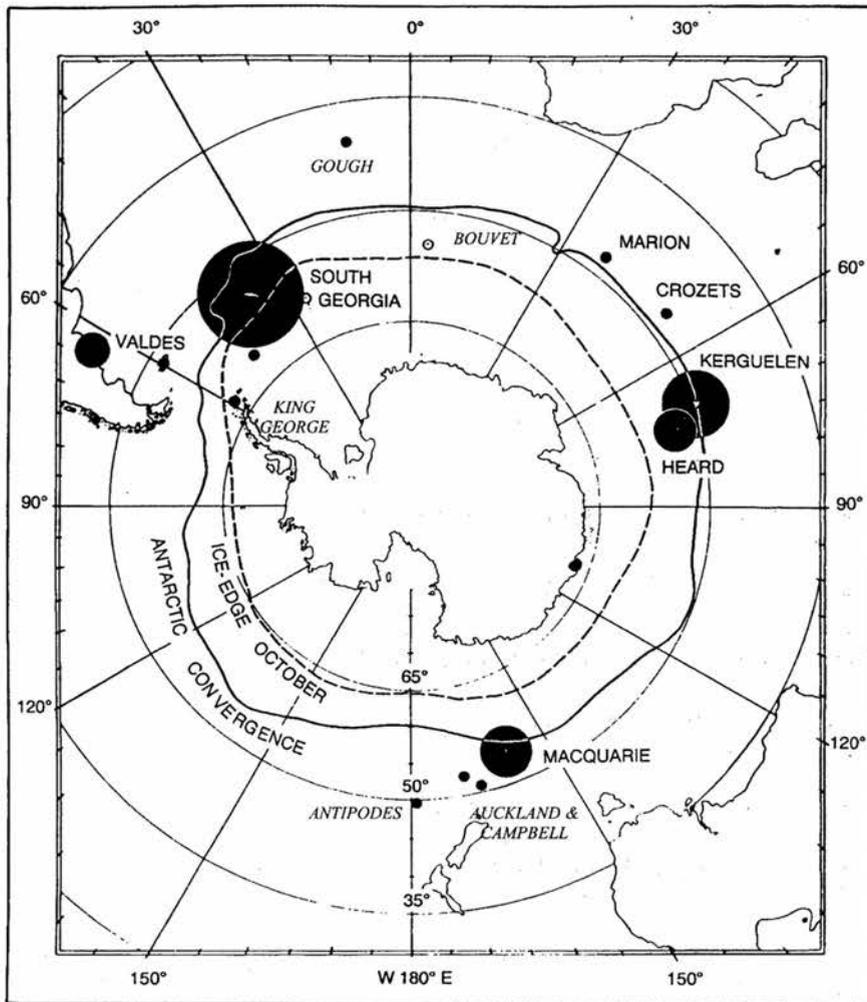


Figure 2. Main haulout sites for southern elephant seals. Closed circles indicate known breeding sites, while open circles indicate probable small breeding sites. Circle sizes are proportional to the estimated population sizes for populations ≥ 5000 individuals. (Source: Laws, 1994)

Global distribution and population trends

Historically, three main stocks of Southern elephant seals were identified: South Georgia, Kerguelen and Macquarie Island (Laws, 1994). Recent research has concluded that elephant seals at Peninsula Valdes in southern Argentina are genetically distinct from the South Georgia stock (Hoelzel et al., 2001; Slade et al., 1998). These main stocks together form a virtually circumpolar distribution throughout the Southern Ocean (Figure 2), and although they are considered different

genetic stocks (Slade et al., 1998), one recent study suggests that long-range gene flow may occur (Fabiani et al., 2003).

The total population size reported in Laws (1994) was 664,000, but a more recent estimate is slightly higher at about 740,000 (McMahon, 2002) and Table 1. The largest stock is that of the South Atlantic sector of the SO, including South Georgia and smaller populations on islands such as Bouvet, King George, South Orkney and the Falkland Islands (Figure 2). Almost 99 % of this stock belongs to the South Georgia population, and represents about 55 % of the total world population (Table 1). The Península Valdes stock is confined to the Patagonian coast of Argentina, and represents about 10 % of the total South Atlantic populations, or about 6 % of the world population (Table 1). The stock in the Southern Indian Ocean sector of the SO consists of populations on the Kerguelen Islands, Heard, Crozet and Marion & Prince Edward Islands (Figure 1), with the largest populations at Kerguelen (~144,000) and Heard Island (~40,000). This stock represents about 28 % of the world population (Table 1). Lastly, the main focus of this thesis is the Macquarie Island stock in the South-western Pacific sector of the SO (Figure 1). This stock is almost entirely based on Macquarie Island (> 99 %), with only very small numbers breeding at Campbell and Antipodes Islands. The most recent estimate for the Macquarie Island population is 76,000 (McMahon, 2002).

Stock	Population	Population size	Reference	Trend
South Georgia	South Georgia	397,054	(Boyd et al., 1996)	—
	South Orkney I.	20	(Laws, 1994)	?
	South Shetland Is.	2,300	(Laws, 1994)	?
	Falkland Is.	1,827	(Galimberti and Boitani, 1999)	—
	Gough I.	63	(Bester et al., 2001)	↓
	Bouvetøya	308	(Kirkman et al., 2001)	↑ (?)
All	401,572			
Península Valdes	Península Valdes	42,371	(Lewis et al., 1998)	↑
	All	42,371		
Kerguelen	Îles Kerguelen	153,237	(Guinet et al., 1999)	—
	Heard I.	61,933	(Slip and Burton, 1999)	—
	Marion I.	2,009	(Laws, 1994)	↓ / —
	Prince Edward I.	782	(Laws, 1994)	?
	Île Crozet	1,995	(Guinet et al., 1999)	?
All	219,956			
Macquarie I.	Macquarie I.	76,000	(McMahon, 2002)	↓ (?)
	Campbell I.	20	(Laws, 1994)	↓ (?)
	Antipodes I.	400	(Laws, 1994)	— (?)
	All	76,420		
World		740,319		↑ (?)

Table 1. Summary of estimated population sizes of southern elephant seals, slightly modified from McMahon (2002).

Southern elephant seals were harvested at all their major breeding grounds well into the 1900s (Carrick et al., 1962; Laws, 1994; McCann, 1985; McCann and Rothery, 1988; van Aarde, 1980). The harvesting of elephant seals at South Georgia and Macquarie ceased in the mid-1960s (Hindell and Burton, 1987; McCann, 1985), while

harvesting ceased by the 1920s at Kerguelen (except for limited operations from 1958 – 1964) due to severely depleted numbers (van Aarde, 1980). Since then, these different populations have developed very differently. The size of the South Georgia stock appears to have remained more or less stable since 1951 (Boyd et al., 1996; McCann and Rothery, 1988). The Kerguelen stock (including Heard & Macdonald, Crozet and Marion & Prince Edward Islands) went through a dramatic decline of ~ 50 % during the 1950s (e.g. Bester, 1988; Bester and Wilkinson, 1994; Burton, 1986; van Aarde, 1980), but now appears to have stabilised at most breeding sites (e.g. Guinet et al., 1999; Pistorius et al., 2001; Slip and Burton, 1999). The changes in the Macquarie stock are described in detail in the following section.

Macquarie Island stock

After the closure of the elephant seal industry at Macquarie Island in the mid-1960s, the population continued to decrease over the following 30 years or so. The estimated population size in 1949 was 183,000, decreasing to 156,000 in 1959 and 86,500 in 1985 (Hindell and Burton, 1987). The population size is currently estimated to ~ 76,000 (McMahon, 2002), resulting in an estimated decline of almost 60 % since 1949. Hindell and Burton (1987) estimated the annual rate of decline to ~ 2.1 % between 1949 and 1985. Recent estimates suggest that between 1985 and 1998 this rate was slightly lower (~ 1.7 %, Australian Antarctic Division, unpublished data). The ultimate reasons for this decline remain largely unexplained. However, the main cause appears to have been a dramatic decrease in first-year survival observed during the 1960's (to less than 2 % in 1965) while survival of other age groups remained more or less constant (Hindell, 1991). This dramatic change is likely to have resulted in drastically reduced rates of breeding recruitment in subsequent years, and it has

been suggested that this may have been responsible for the sustained population decline after the 1960's (Hindell, 1991).

The fact that the reduction in survival during the 1960's was limited to first-year seals would suggest that, irrespective of the nature of the cause (e.g. disease, inter- or intra-specific competition for food, predation, interaction with fisheries, medium- or large-scale environmental change), it acted mainly on this age class. Consequently, much subsequent research at Macquarie has focused on the behaviour, growth and survival of first-year seals e.g. (Bell et al., 1997; Biuw et al., 2003; Hindell et al., 1999; Irvine et al., 2000; McConnell et al., 2002; McMahon et al., 1999, 2000a), and this growing body of information is complemented by studies of this age class from other populations of southern elephant seals [Arnbom, 1993 #24; Carlini, 2000 #16; Carlini, 2001 #15] as well as northern elephant seals (Houser and Costa, 2001; Kretzmann et al., 1991; Kretzmann et al., 1993; Noren et al., 2003; Rea and Costa, 1992).

McMahon et al. (2000a) showed that first-year survival was positively related to their mass at weaning. Based on detailed and long-term life-history studies of a variety of demographic variables, McMahon (2002) concluded that the factors with the highest influence on population trends were (in order of decreasing importance) 1) juvenile survival, 2) adult survival, 3) adult fecundity and 4) juvenile fecundity. Survival analyses have also revealed that age-specific probability of survival at Macquarie Island fluctuates dramatically over the first 3-4 years of life (McMahon et al., 2003). First-year survival probability (~ 0.75) is comparable to other populations studied, and increases to ~ 0.85 in the second year, but by the third year it has again decreased dramatically (0.75), before it appears to stabilise at a relatively high probability (~ 0.80) from the fourth year onwards. While first-year survival appears to be related to

weaning mass (see references above), these later fluctuations in survival seem to less correlated to the initial body condition, and it is likely that they are instead more closely linked to environmental variation in for instance prey availability and individual responses to this variation. This again highlights the importance of analysing these demographic processes within an environmental and oceanographic framework.

The Southern Ocean

Physical oceanography

The Southern Ocean is a continuous circumpolar ocean system that surrounds the entire Antarctic continent and forms a continuous link between the other main oceans of the world. Formally, the northern extent of the Southern Ocean (SO) is defined as the 60th parallel south, while the southern extent is defined as the Antarctic coastline (International Hydrographic Organization, 2000). The management of the biological resources within the SO is the responsibility of the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR), and extends further north in some areas than the formal limits (Figure 3).



- STATISTICAL AREA
 ZONE STATISTIQUE
 ЦИТАТИВНИСКИЕ РАЙОН
 AREA ESTADISTICA
- - - - - STATISTICAL SUBAREA
 ЗОНА ЗОНЕ СТАТИСТИКЕ
 ЦИТАТИВНИСКИЕ СУБРАЙОН
 SUBAREA ESTADISTICA
- - - - - ANTARCTIC CONVERGENCE
 КОНВЕРГЕНЦИЯ АНТАРКТИКЕ
 АНТАРКТИЧЕСКАЯ КОНВЕРГЕНЦИЯ
 CONVERGENCIA ANTARCTICA
- CONTINENT, ISLAND
 КОНТИНЕНТ, ОСТРОВ
 КОНТИНЕНТЕ, ОА
- - - - - INTEGRATED STUDY REGION
 ЗОНА ОУЧЕНЕ ИТЕГРИРЕ
 РАЙОН КОИНСИДЕРИРАЙ ИТЕГРИРАДИ
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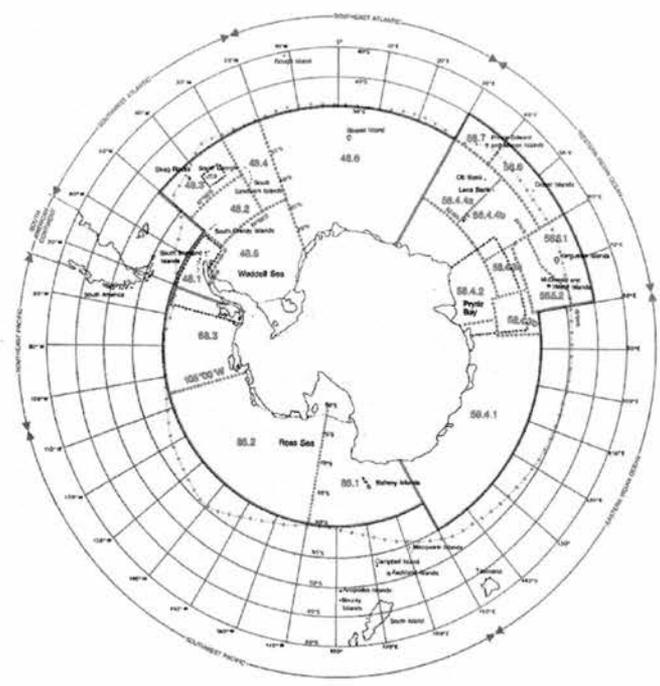


Figure 3. The CCAMLR convention area and sub-areas. (Source: CCAMLR website, <http://www.ccamlr.org/pu/e/gen-intro.htm>)

Oceanographically, the northern extent of the SO can be more accurately defined by the Subantarctic Front (SAF), which marks the northern boundary of the Antarctic Circumpolar Circulation (ACC). The average latitude of the SAF is ~51° S, but it ranges from as far north as around 41° S, just north of the Falkland Islands in the South Atlantic sector, to about 60° S to the west of Drake Passage in the Southeast Pacific sector (Figure 3). As the name implies, the ACC is a circumpolar system of fronts and water masses with an overall eastward drift driven by the predominant westerly winds that characterize the wind patterns of the SO. Following Orsi et al. (1995), the main fronts of the ACC are, in addition to the SAF in the north, the Polar Front (PF) and the Southern ACC Front (sACCF). The southern boundary of the ACC (sbACC) is characterized by an abrupt end to the characteristic signal of the Upper Circumpolar Deep Water (UCDW) as this water mass shoals southward and is entrained into the surface mixed layer (Orsi et al., 1995), and effectively separates the

main eastward drift of the ACC from the west-flowing and weakly sheared water masses of the Antarctic sub-polar regime (Figure 4).

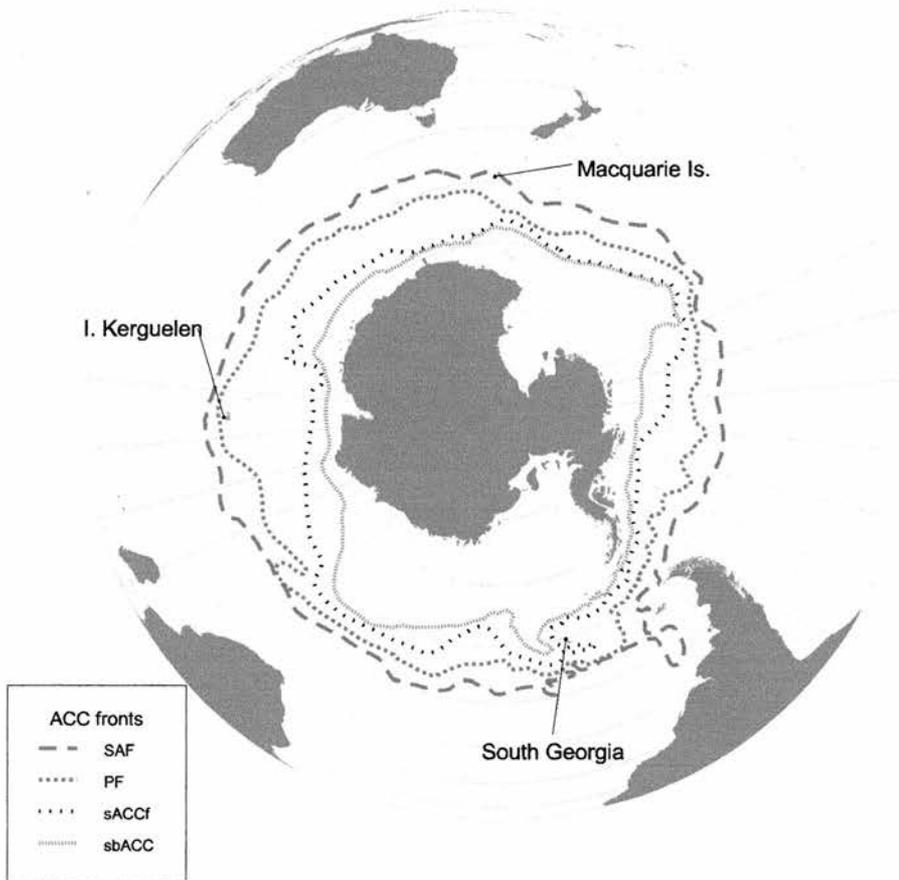


Figure 4. Major frontal systems and boundaries of the Antarctic Circumpolar Circulation (ACC), adapted from Orsi et al. (1995). SAF = Sub-Antarctic front, PF = Polar Front, sACCf = southern ACC Front and sbACC = southern boundary of the ACC.

The longitudinal and meridional location of the major frontal systems and boundaries between water bodies are strongly influenced by water depth, and vary substantially between sectors of the Southern Ocean with different bottom topographies (Orsi et al., 1995). In the Southwestern sector of the SO, the meridional extent of the ACC is

severely reduced due to the presence of the South Pacific Ridge system to the south and east of New Zealand (Orsi et al., 1995, see Figure 4). The physical properties of the SO water masses are not constant, but vary seasonally as well as between years. Significant inter-annual variations in the atmospheric pressure at sea level, wind stress, sea surface temperature and sea-ice extent over the Southern Ocean have been identified, and these anomalies appear to propagate eastward with a period of 4-5 years, taking 8-10 years to encircle the pole (White and Peterson, 1996). This system of coupled anomalies, now commonly referred to as the Antarctic Circumpolar Wave (ACW), play an important role in climate regulation and dynamics within the SO, and has been shown to be linked with global ocean and atmospheric processes such as the El Niño Southern Oscillation (ENSO) (Kwok and Comiso, 2002; Peterson and White, 1998; White et al., 2002).

Biological oceanography

The ACC plays a vital role in the Southern Ocean ecosystem. The transport and mixing occurring at boundaries and frontal systems within the ACC are frequently associated with enhanced primary production (e.g. Hiscock et al., 2003; Pollard et al., 2002; Ward et al., 2002). This enhanced productivity in turn supports a large biomass of organisms ranging from zooplankton to top predators such as seabirds, seals and cetaceans that accumulate in these productive regions (Guinet et al., 2001; McConnell et al., 2002; Tynan, 1998). Changes in these environmental parameters, caused by for instance the ACW, can have dramatic effects on the distribution and survival of upper trophic predators (Barbraud et al., 2000; McCafferty et al., 1998).

Summary

Based on current theory and previous results from extensive studies on southern elephant seals and, to some extent, their northern counterparts, we suggest that rather than searching for simply linear functional relationships, we may expect that the life history and reproductive strategies of elephant seals are modified by a series of size/condition thresholds acting at critical stages throughout their lives:

The first of these thresholds may act already before pups are born (Arnbom et al., 1994), causing the slightly skewed birth sex ratio among small mothers. This mechanism will not be further examined in this thesis.

A second threshold may influence the probability of survival over the first year. Although it has already been shown that this probability is related to the mass of pups at weaning (McMahon et al., 2003), it is not mass *per se* that is important, but rather what it consists of in terms of the relative amount of energy stores and somatic tissue. Also, the exact form of this relationship is not clear, but if there is a threshold, we may see a steep increase over the lower end of body conditions, and a gradual flattening at the upper end, and we may also expect the shape of this function to be different between male and female pups.

A possible third threshold may be involved in the probability of individuals attaining reproductive age. As discussed above, this probability may not be directly linked to body mass/condition at weaning, but we may expect that factors such as growth and early foraging experience over the first year may influence the subsequent fate of individuals. Although this is outside the scope of this thesis, data on the behavioural and physiological changes over the first year presented here may be valuable for ongoing studies into the links between survival, body condition and foraging

behaviour over the subsequent juvenile years (Antarctic Wildlife Research Unit and Australian Antarctic Division, work in progress).

References

- Albon, S. D., and T. H. Clutton-Brock. 1988. Climate and the population dynamics of red deer in Scotland. In M. B. Usher and D. B. A. Thompson (eds.), *Ecological changes in the Uplands*, pp. 93-107. Blackwell Scientific Publications, Oxford.
- Albon, S. D., T. N. Coulson, D. Brown, F. E. Guinness, J. M. Pemberton, and T. H. Clutton-Brock. 2000. Temporal changes in key factors and key age groups influencing the population dynamics of female red deer. *Journal of Animal Ecology*, 69:1099-1110.
- Alexander, R. D., J. L. Hoogland, R. D. Howard, K. M. Noonan, and P. W. Sherman. 1979. Sexual dimorphism and breeding systems in pinnipeds, ungulates, primates and humans. In N. A. Chagnon and W. Irons (eds.), *Evolutionary biology and human social behaviour*, pp. 432-435. Duxbury Press, North Scituate.
- Anderson, S. S., and M. A. Fedak. 1985. Grey seal males: energetic and behavioural links between size and sexual success. *Animal Behaviour*, 33:829-838.
- . 1987. Grey seal energetics: females invest more in male offspring. *Journal of Zoology*, 211:667-679.
- Arnborn, T. 1994. Maternal investment in male and female offspring in the southern elephant seals. PhD thesis, Department of Zoology, Stockholm University, Sweden.
- Arnborn, T., M. A. Fedak, and I. L. Boyd. 1997. Factors affecting maternal expenditure in southern elephant seals during lactation. *Ecology*, 78:471-483.
- Arnborn, T., M. A. Fedak, I. L. Boyd, and B. J. McConnell. 1993. Variation in Weaning Mass of Pups in Relation to Maternal Mass, Postweaning Fast Duration, and Weaned Pup Behavior in Southern Elephant Seals (*Mirounga-Leonina*) At South-Georgia. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 71:1772-1781.
- Arnborn, T., M. A. Fedak, and P. Rothery. 1994. Offspring Sex-Ratio in Relation to Female Size in Southern Elephant Seals, *Mirounga-Leonina*. *Behavioral Ecology and Sociobiology*, 35:373-378.
- Arnould, J. P. Y., I. L. Boyd, and D. G. Socha. 1996. Milk consumption and growth efficiency in Antarctic fur seal (*Arctocephalus gazella*) pups. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 74:254-266.
- Baker, J. D., and C. W. Fowler. 1992. Pup Weight and Survival of Northern Fur Seals *Callorhinus-Ursinus*. *Journal of Zoology*, 227:231-238.
- Barbraud, C., H. Weimerskirch, C. Guinet, and P. Jouventin. 2000. Effect of sea-ice extent on adult survival of an Antarctic top predator: the snow petrel *Pagodroma nivea*. *Oecologia*, 125:483-488.
- Beauplet, G., C. Guinet, and J. P. Y. Arnould. 2003. Body composition changes, metabolic fuel use, and energy expenditure during extended fasting in subantarctic fur seal (*Arctocephalus tropicalis*) pups at Amsterdam Island. *Physiological and Biochemical Zoology*, 76:262-270.
- Beck, C. A., W. D. Bowen, and S. J. Iverson. 2000. Seasonal changes in buoyancy and diving behaviour of adult grey seals. *Journal of Experimental Biology*, 203:2323-2330.
- . 2003. Sex differences in the seasonal patterns of energy storage and expenditure in a phocid seal. *Journal of Animal Ecology*, 72:280-291.

- Bell, C. M., H. R. Burton, and M. A. Hindell. 1997. Growth of southern elephant seals, *Mirounga leonina*, during their first foraging trip. *Australian Journal of Zoology*, 45:447-458.
- Bennett, K. A., B. J. McConnell, and M. A. Fedak. 2001. Diurnal and seasonal variations in the duration of depth of the longest dives in southern elephant seals (*Mirounga leonina*): possible physiological and behavioural constraints. *Journal of Experimental Biology*:649-662.
- Bérubé, C. H., M. Festa-Bianchet, and J. T. Jorgenson. 1996. Reproductive costs of sons and daughters in Rocky Mountain bighorn sheep. *Behavioral Ecology*, 7:60-68.
- Bester, M. N. 1988. Marking and Monitoring Studies of the Kerguelen Stock of Southern Elephant Seals *Mirounga-Leonina* and Their Bearing On Biological-Research in the Vestfold Hills. *Hydrobiologia*, 165:269-277.
- Bester, M. N., H. Moller, J. Wium, and B. Enslin. 2001. An update on the status of southern elephant seals at Gough Island. *South African Journal of Wildlife Research*, 31:68-71.
- Bester, M. N., and I. S. Wilkinson. 1994. Population ecology of southern elephant seals at Marion Island. In B. J. L. LeBoeuf, R. M. (ed.), *Elephant Seals*, pp. 85-97. University of California Press, Los Angeles.
- Birgersson, B. 1998. Male-biased maternal expenditure and associated costs in fallow deer. *Behavioral Ecology and Sociobiology*, 43:87-93.
- Birgersson, B., and K. Ekvall. 1997. Early growth in male and female fallow deer fawns. *Behavioral Ecology*, 8:493-499.
- Biuw, M., B. McConnell, C. J. A. Bradshaw, H. Burton, and M. Fedak. 2003. Blubber and buoyancy: Monitoring the body condition of free-ranging seals using simple dive characteristics. *Journal of Experimental Biology*, 206:3405-3423.
- Bowen, W. D., S. J. Iverson, D. J. Boness, and O. T. Oftedal. 2001. Foraging effort, food intake and lactation performance depend on maternal mass in a small phocid seal. *Functional Ecology*, 15:325-334.
- Bowen, W. D., W. T. Stobo, and S. J. Smith. 1992. Mass Changes of Gray Seal *Halichoerus-Grypus* Pups On Sable Island - Differential Maternal Investment Reconsidered. *Journal of Zoology*, 227:607-622.
- Boyd, I. L., T. A. Arnborn, and M. A. Fedak. 1994. Biomass and energy consumption of the South Georgia stock of southern elephant seals. In B. J. Le Boeuf and R. M. Laws (eds.), *Elephant Seals*, pp. 98-120. University of California Press, Los Angeles.
- Boyd, I. L., J. P. Croxall, N. J. Lunn, and K. Reid. 1995. Population Demography of Antarctic Fur Seals - the Costs of Reproduction and Implications For Life-Histories. *Journal of Animal Ecology*, 64:505-518.
- Boyd, I. L., T. R. Walker, and J. Poncet. 1996. Status of southern elephant seals at South Georgia. *Antarctic Science*, 8:237-244.
- Bradshaw, C. J. A., R. J. Barker, R. G. Harcourt, and L. S. Davis. 2003. Estimating survival and capture probability of fur seal pups using multistate mark-recapture models. *Journal of Mammalogy*, 84:65-80.
- Braza, F., C. San Jose, and S. Aragon. 2000. Variation of male-biased maternal investment in fallow deer (*Dama dama*). *Journal of Zoology*, 250:237-241.
- Burton, H. 1986. A substantial decline in numbers of the southern elephant seal at Heard Island. *Tasmanian Naturalist*, 86:4-8.

- Campagna, C., B. J. Le Boeuf, M. Lewis, and C. Bisioli. 1992. Equal Investment in Male and Female Offspring in Southern Elephant Seals. *Journal of Zoology*, 226:551-561.
- Carlini, A. R., M. E. I. Márquez, S. Ramdohr, H. Bornemann, H. O. Panarello, and G. A. Daneri. 2001. Postweaning Duration and Body Composition Changes in Southern Elephant Seal (*Mirounga leonina*) Pups at King George Island. *Physiological and Biochemical Zoology*, 74:531-540.
- Carrick, R., S. E. Csordas, S. E. Ingham, and K. Keith. 1962. Studies on the Southern Elephant seal, *Mirounga leonina* (L.). *CSIRO (Commonwealth Scientific and Industrial Research Organization Division of Fisheries and Oceanography) Wildlife Research*, 7:161-197.
- Clutton-Brock, T., and C. Godfray. 1991. Parental investment. In J. R. Krebs and N. B. Davis (eds.), *Behavioural ecology: an evolutionary approach*, pp. 234-262. Blackwell Scientific, Oxford.
- Clutton-Brock, T. H. 1988. Reproductive success. In T. H. Clutton-Brock (ed.), *Reproductive success*, pp. 472-485. University of Chicago Press, Chicago and London.
- Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon. 1983. The costs of reproduction to red deer hinds. *Journal of Animal Ecology*, 52:2367.
- Clutton-Brock, T. H., O. F. Price, S. D. Albon, and P. A. Jewell. 1992. Early development and population fluctuations in Soay sheep. *Journal of Animal Ecology*, 61:381-396.
- Côté, S. D., and M. Festa-Bianchet. 2001. Birthdate, mass and survival in mountain goat kids: effects of maternal characteristics and forage quality. *Oecologia*, 127:230-238.
- Coulson, T., E. A. Catchpole, S. D. Albon, B. J. T. Morgan, J. M. Pemberton, T. H. Clutton-Brock, M. J. Crawley, and B. T. Grenfell. 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. *Science*, 292:1528-1531.
- Crocker, D. E., J. D. Williams, D. P. Costa, and B. J. Le Boeuf. 2001. Maternal traits and reproductive effort in northern elephant seals. *Ecology*, 82:3541-3555.
- Derocher, A. E., and I. Stirling. 1998. Maternal investment and factors affecting offspring size in polar bears (*Ursus maritimus*). *Journal of Zoology*, 245:253-260.
- Donohue, M. J., D. P. Costa, E. Goebel, G. A. Antonelis, and J. D. Baker. 2002. Milk intake and energy expenditure of free-ranging northern fur seal, *Callorhinus ursinus*, pups. *Physiological and Biochemical Zoology*, 75:3-18.
- Fabiani, A., A. R. Hoelzel, F. Galimberti, and M. M. C. Muelbert. 2003. Long-range paternal gene flow in the southern elephant seal. *Science*, 299:676-676.
- Fedak, M. A., and S. S. Anderson. 1982. The energetics of lactation: accurate measurements from a large wild mammal, the grey seal (*Halichoerus grypus*). *Journal of Zoology*, 198:473-479.
- Fedak, M. A., T. Arnborn, and I. L. Boyd. 1996. The relation between the size of southern elephant seal mothers, the growth of their pups, and the use of maternal energy, fat and protein during lactation. *Physiological Zoology*, 69:887-911.
- Festa-Bianchet, M., J. M. Gaillard, and J. T. Jorgenson. 1998. Mass- and density-dependent reproductive success and reproductive costs in a capital breeder. *American Naturalist*, 152:367-379.

- Festa-Bianchet, M., J. T. Jorgenson, W. J. King, K. G. Smith, and W. D. Wishart. 1996. The development of sexual dimorphism: seasonal and lifetime mass changes in bighorn sheep. *Canadian Journal of Zoology*, 74:330-342.
- Festa-Bianchet, M., J. T. Jorgenson, M. Lucherini, and W. D. Wishart. 1995. Life-History Consequences of Variation in Age of Primiparity in Bighorn Ewes. *Ecology*, 76:871-881.
- Fisher, R. A. 1930. *The genetical theory of natural selection*. Oxford University Press, Oxford.
- Gaillard, J. M., M. Festa-Bianchet, D. Delorme, and J. Jorgenson. 2000. Body mass and individual fitness in female ungulates: bigger is not always better. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 267:471-477.
- Galimberti, F., and L. Boitani. 1999. Demography and breeding biology of a small, localized population of southern elephant seals (*Mirounga leonina*). *Marine Mammal Science*, 15:159-178.
- Gentry, R. 1999. *Behaviour and Ecology of the Northern Fur Seal*. Princeton University Press.
- Guinet, C., L. Dubroca, M. A. Lea, S. Goldsworthy, Y. Cherel, G. Duhamel, F. Bonadonna, and J. P. Donnay. 2001. Spatial distribution of foraging in female Antarctic fur seals *Arctocephalus gazella* in relation to oceanographic variables: a scale-dependent approach using geographic information systems. *Marine Ecology-Progress Series*, 219:251-264.
- Guinet, C., P. Jouventin, and H. Weimerskirch. 1999. Recent population change of the southern elephant seal at Iles Crozet and Iles Kerguelen: the end of the decrease? *Antarctic Science*, 11:193-197.
- Ha, J. C., R. L. Robinette, and G. P. Sackett. 2000. Demographic analysis of the Washington Regional Primate Research Center pigtailed macaque colony, 1967-1996. *American Journal of Primatology*, 52:187-198.
- Haley, M. P., C. J. Deutsch, and B. J. Le Boeuf. 1994. Size, Dominance and Copulatory Success in Male Northern Elephant Seals, *Mirounga-Angustirostris*. *Animal Behaviour*, 48:1249-1260.
- Hindell, M. A. 1991. Some Life-History Parameters of a Declining Population of Southern Elephant Seals, *Mirounga-Leonina*. *Journal of Animal Ecology*, 60:119-134.
- Hindell, M. A., and H. R. Burton. 1987. Past and present status of the southern elephant seal (*Mirounga leonina* Linn.) at Macquarie Island. *Journal of Zoology*, 213:365-380.
- Hindell, M. A., B. J. McConnell, M. A. Fedak, D. J. Slip, H. R. Burton, P. J. H. Reijnders, and C. R. McMahon. 1999. Environmental and physiological determinants of successful foraging by naive southern elephant seal pups during their first trip to sea. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 77:1807-1821.
- Hindell, M. A., and C. R. McMahon. 2000. Long distance movement of a southern elephant seal (*Mirounga leonina*) from Macquarie Island to Peter 1 Oy. *Marine Mammal Science*, 16:504-507.
- Hindell, M. A., D. J. Slip, and H. R. Burton. 1991. The Diving Behavior of Adult Male and Female Southern Elephant Seals, *Mirounga-Leonina* (Pinnipedia, Phocidae). *Australian Journal of Zoology*, 39:595-619.
- Hindell, M. A., D. J. Slip, H. R. Burton, and M. M. Bryden. 1992. Physiological Implications of Continuous, Prolonged, and Deep Dives of the Southern

- Elephant Seal (*Mirounga-Leonina*). *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 70:370-379.
- Hiscock, M. R., J. Marra, W. O. Smith, R. Goericke, C. Measures, S. Vink, R. J. Olson, H. M. Sosik, and R. T. Barber. 2003. Primary productivity and its regulation in the Pacific Sector of the Southern Ocean. *Deep-Sea Research Part II-Topical Studies in Oceanography*, 50:533-558.
- Hoelzel, A. R., C. Campagna, and T. Arnborn. 2001. Genetic and morphometric differentiation between island and mainland southern elephant seal populations. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 268:325-332.
- Hoelzel, A. R., B. J. Le Boeuf, J. Reiter, and C. Campagna. 1999. Alpha-male paternity in elephant seals. *Behavioral Ecology and Sociobiology*, 46:298-306.
- Houser, D. S., and D. P. Costa. 2001. Protein catabolism in suckling and fasting northern elephant seal pups (*Mirounga angustirostris*). *J Comp Physiol B*, DOI 10.1007/s003600100214.
- Houston, A. I., and J. M. McNamara. 1993. A Theoretical Investigation of the Fat Reserves and Mortality Levels of Small Birds in Winter. *Ornis Scandinavica*, 24:205-219.
- Irvine, L. G., M. A. Hindell, J. van den Hoff, and H. R. Burton. 2000. The influence of body size on dive duration of underyearling southern elephant seals (*Mirounga leonina*). *Journal of Zoology*, 251:463-471.
- Jonker, F. C., and M. N. Bester. 1998. Seasonal movements and foraging areas of adult southern female elephant seals, *Mirounga leonina*, from Marion Island. *Antarctic Science*, 10:21-30.
- Jorgenson, J. T., M. Festa-Bianchet, M. Lucherini, and W. D. Wishart. 1993. Effects of Body-Size, Population-Density, and Maternal Characteristics On Age At First Reproduction in Bighorn Ewes. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 71:2509-2517.
- Keech, M. A., R. T. Bowyer, J. M. Ver Hoef, R. D. Boertje, B. W. Dale, and T. R. Stephenson. 2000. Life-history consequences of maternal condition in Alaskan moose. *Journal of Wildlife Management*, 64:450-462.
- Kirkman, S. P., G. J. G. Hofmeyr, M. N. Bester, and K. Isaksen. 2001. Counts of southern elephant seals, *Mirounga leonina*, at Bouvet Island. *Polar Biology*, 24:62-65.
- Kohlmann, S. G. 1999. Adaptive fetal sex allocation in elk: Evidence and implications. *Journal of Wildlife Management*, 63:1109-1117.
- Kovacs, K. M., and D. M. Lavigne. 1986. Growth of grey seal *Halichoerus grypus* neonates: differential maternal investment in the sexes. *Canadian Journal of Zoology - Revue Canadienne de Zoologie*, 64:1937-1943.
- Kretzmann, M. B., D. P. Costa, L. V. Higgins, and D. J. Needham. 1991. Milk composition of Australian sea lions, *Neophoca cinerea*: variability in lipid content. *Canadian Journal of Zoology*, 69:2556-2561.
- Kretzmann, M. B., D. P. Costa, and B. J. Le Boeuf. 1993. Maternal Energy Investment in Elephant Seal Pups - Evidence For Sexual Equality. *American Naturalist*, 141:466-480.
- Kruuk, L. E. B., T. H. Clutton-Brock, S. D. Albon, J. M. Pemberton, and F. E. Guinness. 1999. Population density affects sex ratio variation in red deer. *Nature*, 399:459-461.
- Kruuk, L. E. B., T. H. Clutton-Brock, J. Slate, J. M. Pemberton, S. Brotherstone, and F. E. Guinness. 2000. Heritability of fitness in a wild mammal population.

- Proceedings of the National Academy of Sciences of the United States of America*, 97:698-703.
- Kwok, R., and J. C. Comiso. 2002. Southern Ocean climate and sea ice anomalies associated with the Southern Oscillation. *Journal of Climate*, 15:487-501.
- Laurenson, M. K. 1995. Cub growth and maternal care in cheetahs. *Behavioral Ecology*, 6:405-409.
- Laws, R. M. 1953. A new method of age determination in mammals with special reference to the elephant seal (*Mirounga leonina*). *Falkld Isl. Depend. Surv. Rep*; 2:1-11.
- . 1994. History and present status of southern elephant seals populations. In B. J. LeBoeuf and R. M. Laws (eds.), *Elephant Seals*, pp. 49-65. University of California Press, Los Angeles.
- Le Boeuf, B. J. 1974. Male-male competition and reproductive success in elephant seals. *American Zoology*, 14:163-176.
- Le Boeuf, B. J., R. Condit, and J. Reiter. 1989. Parental Investment and the Secondary Sex-Ratio in Northern Elephant Seals. *Behavioral Ecology and Sociobiology*, 25:109-117.
- Le Boeuf, B. J., and J. Reiter. 1988. Lifetime reproductive success in northern elephant seals. In T. H. Clutton-Brock (ed.), *Reproductive success*, pp. 344-362. University of Chicago Press, Chicago and London.
- Lee, P. C., and C. J. Moss. 1986. Early Maternal Investment in Male and Female African Elephant Calves. *Behavioral Ecology and Sociobiology*, 18:353-361.
- Lewis, M., C. Campagna, F. Quintana, and V. Falabella. 1998. Estado actual y distribucion de la poblacion elefante marino del sur en la Peninsula Valdes, Argentina. *Mastozoologia Neotropical*, 5:29-40.
- Lima, S. L. 1986. Predation Risk and Unpredictable Feeding Conditions - Determinants of Body-Mass in Birds. *Ecology*, 67:377-385.
- Lindfors, P., B. S. Tullberg, and M. Biuw. 2002. Phylogenetic analyses of sexual selection and sexual size dimorphism in pinnipeds. *Behavioral Ecology and Sociobiology*, 52:188-193.
- Ling, J. K., and M. M. Bryden. 1981. Southern elephant seal *Mirounga leonina* Linnaeus, 1758. In S. H. Ridgway and R. J. Harrison (eds.), *Handbook of Marine Mammals*, Vol. 2: Seals, pp. 297-327. Academic Press, London.
- Lunn, N. J., I. L. Boyd, and J. P. Croxall. 1994. Reproductive-Performance of Female Antarctic Fur Seals - the Influence of Age, Breeding Experience, Environmental Variation and Individual Quality. *Journal of Animal Ecology*, 63:827-840.
- Marker, L. L., A. J. Dickman, R. M. Jeo, M. G. L. Mills, and D. W. Macdonald. 2003. Demography of the namibian cheetah, *Acinonyx jubatus jubatus*. *Biological Conservation*, 114:413-425.
- Maynard Smith, J. 1980. A new theory of sexual investment. *Behavioral Ecology and Sociobiology*, 7:247-251.
- McCafferty, D. J., I. L. Boyd, T. R. Walker, and R. I. Taylor. 1998. Foraging responses of Antarctic fur seals to changes in the marine environment. *Marine Ecology-Progress Series*, 166:285-299.
- McCann, T. S. 1985. Size, status and demography of southern elephant seal (*Mirounga leonina*) populations. In J. K. Ling and M. M. Bryden (eds.), *Studies of Sea Mammals in South Latitudes*, pp. 1-17. South Australian Museum, Sydney.

- McCann, T. S., W. N. Bonner, J. H. Prime, and C. Ricketts. 1979. Age distribution and age at first pregnancy of South Georgia elephant seals. *ICES CM* 1979/N:13.
- McCann, T. S., M. A. Fedak, and J. Harwood. 1989. Parental Investment in Southern Elephant Seals, *Mirounga leonina*. *Behavioral Ecology and Sociobiology*, 25:81-87.
- McCann, T. S., and P. Rothery. 1988. Population size and status of the southern elephant seal (*Mirounga leonina*) at South Georgia, 1951-85. *Polar Biology*, 8:305-309.
- McConnell, B. J., and M. A. Fedak. 1996. Movements of southern elephant seals. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 74:1485-1496.
- McConnell, B. J., M. A. Fedak, H. R. Burton, G. H. Englehard, and P. Reijnders. 2002. Movements and foraging areas of naive, recently weaned southern elephant seal pups. *Journal of Animal Ecology*, 71:65-78.
- McMahon, C. R. 2002. A demographic comparison of two elephant seal populations. PhD thesis, University of Pretoria.
- McMahon, C. R., H. R. Burton, and M. N. Bester. 1999. First-year survival of southern elephant seals, *Mirounga leonina*, at sub-Antarctic Macquarie Island. *Polar Biology*, 21:279-284.
- . 2000a. Weaning mass and the future survival of juvenile southern elephant seals, *Mirounga leonina*, at Macquarie Island. *Antarctic Science*, 12:149-153.
- . 2003. A demographic comparison of two southern elephant seal populations. *Journal of Animal Ecology*, 72:61-74.
- McMahon, C. R., I. C. Field, T. Dorr, D. Washington, and C. Hammond. 2000b. Hook and nose: an interaction between a male elephant seal and a longline fishery. *Polar Record*, 36:250-251.
- Moss, C. J. 2001. The demography of an African elephant (*Loxodonta africana*) population in Amboseli, Kenya. *Journal of Zoology*, 255:145-156.
- Nishida, T., N. Corp, M. Hamai, T. Hasegawa, M. Hiraiwa-Hasegawa, K. Hosaka, K. D. Hunt, N. Itoh, K. Kawanaka, A. Matsumoto-Oda, J. C. Mitani, M. Nakamura, K. Norikoshi, T. Sakamaki, L. Turner, S. Uehara, and K. Zamma. 2003. Demography, female life history, and reproductive profiles among the chimpanzees of Mahale. *American Journal of Primatology*, 59:99-121.
- Noren, D. P., D. E. Crocker, T. M. Williams, and D. P. Costa. 2003. Energy reserve utilization in northern elephant seal (*Mirounga angustirostris*) pups during the postweaning fast: size does matter. *Journal of Comparative Physiology B*, DOI 10.1007/s00360-003-0353-9.
- Orsi, A. H., T. Whitworth, and W. D. Nowlin. 1995. On the Meridional Extent and Fronts of the Antarctic Circumpolar Current. *Deep-Sea Research Part I-Oceanographic Research Papers*, 42:641-673.
- Packer, C., L. Herbst, A. E. Pusey, J. D. Bygott, J. P. Hanby, S. J. Cairns, and M. Borgerhoff-Mulder. 1988. Reproductive success in lions. In T. H. Clutton-Brock (ed.), *Reproductive success*, pp. 363-383. Chicago University Press, Chicago.
- Peterson, R. G., and W. B. White. 1998. Slow oceanic teleconnections linking the Antarctic Circumpolar Wave with the tropical El Nino-Southern Oscillation. *Journal of Geophysical Research-Oceans*, 103:24573-24583.
- Pistorius, P. A., M. N. Bester, S. P. Kirkman, and F. E. Taylor. 2001. Temporal changes in fecundity and age at sexual maturity of southern elephant seals at Marion Island. *Polar Biology*, 24:343-348.

- Pollard, R. T., M. I. Lucas, and J. F. Read. 2002. Physical controls on biogeochemical zonation in the Southern Ocean. *Deep-Sea Research Part II-Topical Studies in Oceanography*, 49:3289-3305.
- Pomeroy, P. P., M. A. Fedak, P. Rothery, and S. Anderson. 1999. Consequences of maternal size for reproductive expenditure and pupping success of grey seals at North Rona, Scotland. *Journal of Animal Ecology*, 68:235-253.
- Post, J. R., and E. A. Parkinson. 2001. Energy allocation strategy in young fish: Allometry and survival. *Ecology*, 82:1040-1051.
- Rea, L. D., and D. P. Costa. 1992. Changes in standard metabolism during long-term fasting in northern elephant seal pups (*Mirounga angustirostris*). *Physiological Zoology*, 65:97-111.
- Rogers, C. M. 1987. Predation risk and fasting capacity: do wintering birds maintain optimal body mass? *Ecology*, 68:1051-1061.
- Rogers, C. M., and R. Heath-Coss. 2003. Effect of experimentally altered food abundance on fat reserves of wintering birds. *Journal of Animal Ecology*, 72:822-830.
- Rogers, C. M., and J. N. M. Smith. 1993. Life-History Theory in the Nonbreeding Period - Trade-Offs in Avian Fat Reserves. *Ecology*, 74:419-426.
- Sauther, M. L., R. W. Sussman, and L. Gould. 1999. The socioecology of the ringtailed lemur: Thirty-five years of research. *Evolutionary Anthropology*, 8:120-132.
- Slade, R. W., C. Moritz, A. R. Hoelzel, and H. R. Burton. 1998. Molecular population genetics of the southern elephant seal *Mirounga leonina*. *Genetics*, 149:1945-1957.
- Slip, D. J., and H. R. Burton. 1999. Population status and seasonal haulout patterns of the southern elephant seal (*Mirounga leonina*) at Heard Island. *Antarctic Science*, 11:38-47.
- Smiseth, P. T., and S. H. Lorentsen. 1995. Evidence of Equal Maternal Investment in the Sexes in the Polygynous and Sexually Dimorphic Grey Seal (*Halichoerus Grypus*). *Behavioral Ecology and Sociobiology*, 36:145-150.
- Smith, J. L. D., and C. McDougal. 1991. The Contribution of Variance in Lifetime Reproduction to Effective Population-Size in Tigers. *Conservation Biology*, 5:484-490.
- Trillmich, F. 1996. Parental Investment in Pinnipeds. *Advanced Study of Behaviour*, 25:533-577.
- Trivers, R. L. 1972. Parental investment and sexual selection. In B. Campbell (ed.), *Sexual Selection and the Descent of Man*, pp. 136-179. Aldine, Chicago.
- Trivers, R. L., and D. E. Willard. 1973. Natural selection of parental ability to vary the sex ratio. *Science*, 179:90-92.
- Tynan, C. T. 1998. Ecological importance of the Southern Boundary of the Antarctic Circumpolar Current. *Nature*, 392:708-710.
- van Aarde, R. J. 1980. Fluctuations in the population of southern elephant seals, *Mirounga leonina*, at Kerguelen Island. *South African Journal of Zoology*, 15:99-106.
- Ward, P., M. Whitehouse, M. Meredith, E. Murphy, R. Shreeve, R. Korb, J. Watkins, S. Thorpe, R. Woodd-Walker, A. Brierley, N. Cunningham, S. Grant, and D. Bone. 2002. The southern antarctic circumpolar current front: physical and biological coupling at South Georgia. *Deep-Sea Research Part I-Oceanographic Research Papers*, 49:2183-2202.

- Webb, P. M., D. E. Crocker, S. B. Blackwell, D. P. Costa, and B. J. Le Boeuf. 1998. Effects of buoyancy on the diving behavior of northern elephant seals. *Journal of Experimental Biology*, 201:2349-2358.
- White, W. B., S. C. Chen, R. J. Allan, and R. C. Stone. 2002. Positive feedbacks between the Antarctic Circumpolar Wave and the global El Nino-Southern Oscillation Wave. *Journal of Geophysical Research-Oceans*, 107:art. no.-3165.
- White, W. B., and R. G. Peterson. 1996. An Antarctic circumpolar wave in surface pressure, wind, temperature and sea-ice extent. *Nature*, 380:699-702.
- Wolff, J. O. 1988. Maternal Investment and Sex-Ratio Adjustment in American Bison Calves. *Journal of Behavioural Ecology and Sociobiology*, 23:127-133.

CHAPTER 2: INDIVIDUAL VARIATION IN BODY COMPOSITION AND METABOLIC REGULATION DURING THE POST-WEANING FAST

Abstract

Phocid seal pups accumulate large amounts of material derived from milk during the short lactation period, and a large fraction of this is lipid. How pups utilise their stored protein and lipid reserves to provide energy after weaning is likely to have crucial impacts on their chances of surviving until they find food. It is generally assumed that individuals with larger absolute lipid stores will have a higher probability of success, but this may be heavily influenced by the ratio of lipid to lean tissue, and the way in which pups utilise various body components for maintenance and growth. We examine the changes in mass and body composition of southern elephant seal pups from Macquarie Island during the post-weaning fasting period on land, in relation to their initial body size and duration of the fast. We deliberately chose individuals to reflect the entire size range of pups at weaning, and consequently weaning mass ranged from 68 to 207 kg (mean: 122.3 ± 30.4 kg). The duration of the fasting period ranged from 14 to 61 days (mean: 38.1 ± 10.8 days), and during this time seals lost between 6 and 68 kg (mean: 33.1 ± 11.6 kg), at a rate of between 0.31 to 1.57 kg/day (mean: 0.86 ± 0.17 kg/day). The rate of mass loss was positively correlated with mass at weaning ($r^2 = 0.74$, $p < 0.001$), and although pups that were larger at weaning were also larger at departure, the relative mass at departure (as a percentage of weaning

mass) was not related to the mass at weaning. However, there was a strong negative relationship between the duration of the fast and the relative departure mass ($r^2 = 0.61$, $p < 0.0001$), and for any given fast duration, pups with a higher weaning mass had a higher relative departure mass compared to pups with a smaller weaning mass. The rate of mass loss decreased throughout the fast. However, there was no clear indication of a switch from normal lipid-based fasting metabolism (i.e. "Phase II" characterised by relatively low rates of mass loss) to a more protein-based fasting (i.e. "Phase III", characterised by higher growth rates). In common with other studies, the energetic contribution of lipid was greater in initially fatter pups. However, the variance in the contribution of lipid decreased markedly with weaning lipid content. This suggests that animals that were relatively fatter at weaning were able to maximise their energy efficiency by catabolising lipid at or close to some maximum rate and still retain a substantial amount of lipid stores at departure. In contrast, leaner animals displayed a continuum of metabolic strategies balancing lipid and protein catabolism and final body composition. While some lean individuals maximised their energy efficiency by having a relatively high energetic contribution of lipid, others sacrifice this efficiency for increased relative energy stores at departure. We also found significant differences between male and female pups in their pattern of resource allocation and partitioning. While there was no difference in the relative contribution of lipid among initially fatter males and females, leaner females had a significantly lower energetic contribution of lipid compared to leaner males. This also resulted in females having significantly higher and much less variable relative lipid contents at departure compared to males. We suggest that the probability of survival once at sea will be strongly influenced by the metabolic strategy employed by a lean

seals during the fast, but this will also be influenced by the predictability and proximity of potential food resources.

Introduction

To understand the complexity of the costs and benefit of parental expenditure, we need to take into account the long-term effects on offspring survival and recruitment into the breeding population. Although this is widely recognised among ecologists and theoretical biologists alike, it has proven a difficult topic to address. Southern elephant seals (*Mirounga leonina*) are ideal subjects for studying these complex linkages, and the long-term decline of the elephant seal population at Macquarie Island (Hindell et al., 1994b) has stimulated research into the effects individual variation in energy expenditure, foraging behaviour and survival may have on population dynamics. There are many theories as to what has caused this decline in the Western Pacific sector of the Southern Ocean while most populations in other sectors are either stable or increasing (Laws, 1994), and differences in juvenile survival between populations may be a contributing factor.

The life history of most seals are characterised by dramatic seasonal changes in body mass and condition. These cycles are particularly dramatic for land-breeding phocids such as elephant seals (*Mirounga* sp.), monk seals (*Monachus* sp.) and some populations of grey seals (*Halichoerus grypus*), because foraging at sea and fasting on land during breeding and moulting are completely separated in space and time. Changes in mass and body composition during these fasting periods can be extreme. For instance, female elephant seals lose >30% of their body mass while lactating (Arnbom et al., 1997; Deutsch et al., 1994), and adult males lose a similar proportion of their body mass during the breeding season (Deutsch et al., 1994).

To reduce the energy deficit while fasting, the lactation period of most female phocids is very short compared to female otariids that return to sea to feed regularly throughout lactation (Trillmich, 1996). As a result, phocid pups have very high growth rates while suckling e.g. (Bowen et al., 1985). These extreme mass gains during periods of lactation that may last only a couple of weeks are a result of extreme accumulations of lipid stores from the very rich milk (Carlini et al., 2000; Hindell et al., 1994a; Houser and Costa, 2001; Lydersen and Kovacs, 1996; Lydersen et al., 1996). For instance, Southern elephant seal pups almost triple their body mass, from 40 - 50 kg at birth to 120 – 160 kg at weaning during the 23-day lactation (Arnbom et al., 1997; Campagna et al., 1992; Carlini et al., 2000; McMahon et al., 2000b), and their lipid content increases from 2 – 3 % at birth to 35 – 45 % at weaning (Carlini et al., 2000; Hindell et al., 1994a). When mothers leave at the end of lactation, pups remain on land fasting for an extended period before they too depart to sea e.g. (Arnbom et al., 1993). During the fasting period, pups expend a large fraction of the energy obtained during lactation, with most of the energy required for maintenance coming from the mobilisation of lipid (Carlini et al., 2001; Carlini et al., 2000; Houser and Costa, 2001; Noren et al., 2003; Rea and Costa, 1992; Reilly, 1991). The high energetic cost and subsequent reserve utilisation during the post-weaning fast is believed to be balanced by benefits resulting from behavioural and physiological changes that improve their swimming and diving ability before departing to sea (Arnbom et al., 1993; Blackwell and Le Boeuf, 1993; Castellini et al., 1994; Thorson and LeBoeuf, 1994). However, the way in which pups utilise their available energy reserves during the fast may have crucial consequences for their at-sea behaviour and early survival. For instance, once southern elephant seal pups depart on their first foraging trip they generally spend the first few weeks travelling at high daily travel

rates in a relatively direct transit before the movements become slower and more meandering, presumably indicating increased searching and/or foraging effort the onset of foraging (Biuw et al., 2003; McConnell et al., 2002). The fasting period is therefore likely to extend well beyond the period on land, and pups departing to sea must have enough stored energy to sustain them throughout the transit to feeding grounds that may be both distant and unpredictable.

Since lipid is the main source of reserve energy and also provides seals with important thermal insulation (Bryden, 1964; Scholander et al., 1950), we may expect that pups with a higher proportion of lipid at departure will have a better chance of reaching the foraging grounds before they deplete their energy stores to critically low levels.

Conservation of lipid reserves during the terrestrial portion of the post-weaning fast would increase the energy stores and thermal insulation, and may therefore incur an advantage once seals depart. However, lipid catabolism is more efficient than protein catabolism in terms of the energy yield from a given unit mass (see for instance (Schmidt-Nielsen, 1997)), and animals with a higher relative contribution of protein for their maintenance would therefore reduce their absolute levels of body materials at a higher rate. This would decrease the overall time an individual could remain on land, and therefore reduce the time available for the potentially survival-enhancing behavioural and physiological changes. Excessive protein catabolism during the post-weaning fast draws on a limited resource, and may result in critical depletion of e.g. cardiac and other muscle tissue (Cahill et al., 1979; Cherel et al., 1987; Reilly, 1989). Even for individuals with abundant reserves of protein rich tissue (such as skeletal muscle), extensive loss of these tissues may be a disadvantage in the medium to long term, particularly in young growing seals. For example, loss of skeletal and cardiac

male and female elephant seals may influence the patterns of resource allocation even in pups. Although such differences have been described for a variety of otariids e.g. (Arnould et al., 1996; Beauplet et al., 2003; Donohue et al., 2002), previous studies on phocids have found no conclusive evidence of sexual differences in changes in body composition throughout lactation (Kretzmann et al., 1993) or the post-weaning fast (Carlini et al., 2001; Noren et al., 2003). Because of their large size and extreme sexual dimorphism, elephant seals are an obvious species in which to look for such differences.

In this paper, we examine individual variations in utilization and allocation of energy and material in newly weaned southern elephant seal pups at Macquarie Island during the post-weaning fast. Specifically, we examine the data for any evidence of metabolic adjustments that allow pups to achieve some desired level of fatness before they depart, and the degree to which such adjustments are linked to other individual factors such as body size and gender. To achieve this, we selected pups to uniformly represent the entire range of body sizes at weaning thereby maximising our ability to describe the effects of individual variation. Based on our results, we also make some predictions of how long individual pups might be able to survive at sea on stored material before they have to find food. We compared our data on changes in body composition and energy expenditure to previous studies on southern (Carlini et al., 2001) and northern (Noren et al., 2003) elephant seal pups, and discuss some implications of differences between species and populations.

Materials and Methods

Study site and field procedures

This study was carried out at Macquarie Island in the Southwestern Pacific sector of the Southern Ocean (54° 30'S, 158°57'E) over three seasons (1998 to 2000). We selected our sample from a larger population of individually marked, recently weaned southern elephant seal pups which were also weighed and measured at birth and weaning as part of a large-scale mark/recapture program carried out between 1993 and 2001 e.g. (McMahon et al., 2000b).

Seals were captured and weighed according to (McMahon et al., 2000a). The axial girth was measured just behind the base of the front flippers, and the standard nose-to-tail length was measured as the straight line between the tip of the nose to the tip of the tail. We used isotopically labelled water (e.g. (Nagy and Costa, 1980; Reilly and Fedak, 1990)) to measure the body composition of pups at weaning, prior to departure. Immediately after capture, a blood sample was collected from the extradural vein to measure the background isotope level. A weighed dose of either 4 - 8 ml of deuterium oxide (HDO, specific concentration: 99.9%) or approximately 2 μ Ci tritiated water (^3HHO) in 4 ml of distilled water was then injected using either a 10 ml or 5 ml plastic syringe. The syringe was flushed with blood three times to ensure complete delivery of the labelled water. A second blood sample was taken 2-3 hours after initial injection for determination of dilution space and calculation of body composition. Blood samples were centrifuged and the plasma transferred to 2 ml cryo tubes and these were stored at -20°C until further analysis.

We conducted daily re-sights throughout the study area, and the presence and location of each study animal was noted. We re-captured pups roughly every 10 days to obtain sequential mass and morphometric measurements. The date of departure was predicted using empirically derived relationships between weaning mass, departure mass and daily rate of mass loss (Arnbom et al., 1993). Based on these relationships, we again measured the body composition (using labelled isotope) at a recapture occasion if the mass had decreased by ~25% since weaning. If a pup remained on land more than 1 week after the second body composition measurement, a third measurement was made, and the exact departure date was determined from the daily re-sights.

Laboratory procedures

Tritiated samples

We analyzed plasma samples for ^3H specific activity by liquid scintillation counting. Weighed plasma samples of approximately 100 μl were added to 10 ml of PicoFlour scintillation cocktail (Packard Instruments) and counted in triplicate for 10 minutes on a Packard Tri-Carb® 2000 liquid scintillation counter. Correction for quenching was made by automatic external standardization. We prepared standard dilutions by gravimetric dilution of an aliquot of the injectate to the approximate dilution expected in the seals, and these were also counted in triplicate for 10 min. The exact water content of each plasma sample was determined by transferring ~100 μl of the sample to a weighed glass slide. The slide was weighed again and then dried on a hot plate at a temperature of ~ 50°C until complete evaporation of the plasma water, and the slide was then weighed a third time. In this way we could correct the specific activity of ^3H for the exact plasma water content.

Deuterated samples

Blood samples were distilled using the pipette method of Nagy (1983). Mass spectrometric analysis of deuterium enrichment was performed using H₂ gas, produced from the distilled water after reaction with LiAlH₄ (Ward et al 2000). ²H: ¹H ratios were measured using dual inlet gas source isotope ratio mass spectrometry (Optima, Micromass IRMS), with isotopically characterised gases of H₂ (CP grade gases BOC Ltd) in the reference channel. Reference gases were characterised every 3 months relative to SMOW and SLAP supplied by IAEA. Each batch of samples was run with triplicates of three laboratory standards to correct for day-to-day variation in performance of the mass spectrometers. All isotope enrichments were measured in delta (per mil) relative to the working standards and converted to parts per million (ppm), using the established ratios for these reference materials. Measures of isotope enrichment were based on independent analysis of two sub-samples of the water distilled from the blood samples, which were analysed blind to their biological source.

Statistical and numerical analyses

We used the R package (Ihaka and Gentleman, 1996) for all numerical and statistical data analyses.

Standard diagnostic tests and conversions

We used the Shapiro-Wilks test (`shapiro.test` in the `ctest` library) to determine whether variables were normally distributed. To test for homogeneity of variances between groups of samples we used either of two tests. If variables were normally distributed (see above) we used a standard F-test (`var.test` in the `ctest` package), while if variables were not normally distributed we used a Bartlett test

(bartlett.test in the ctest package). All values are presented as means \pm 1 standard deviation, unless otherwise stated.

Sequential mass changes

To examine more closely how the patterns of mass loss varied throughout the fasting period, we calculated the absolute and mass-specific rates of mass loss over every interval between two consecutive captures. These rates were calculated as:

$$DL = 2 \times \frac{(M_{t-1} - M_t)}{(M_{t-1} + M_t)(t - t_{t-1})} \quad \text{Equation 1}$$

where DL is daily absolute or mass-specific mass loss in $\text{g kg}^{-1} \text{ day}^{-1}$, M_t and M_{t-1} represents mass measurements at two consecutive captures at time $t-1$ and t . This value was then allocated to a day halfway between the two consecutive measurements $t-1$ and t . To determine how these rates changed over the course of fasting while controlling for the lack of independence between repeated measurements on the same individuals, we used linear mixed effects models, as implemented in the nlme package. We tested different models of differing complexity, including days from weaning as well as weaning mass as explanatory variables. To test whether the loss rate changed linearly or non-linearly over time we also included the 2:nd and 3:rd polynomials of days after weaning. In order to compare models with different fixed effects structures, fitting was done using maximum likelihood (ML) rather than the default restricted maximum likelihood (REML) method. Models were compared using Akaike's Information Criterion (AIC, Akaike, 1973), and the "best" model was selected based on Akaike weights (Burnham and Anderson, 1998).

Isotope dilution calculations

We calculated total body water (*TBW*) according to the empirically derived equation for grey seals (Reilly and Fedak, 1990) as:

$$TBW = 0.382 + 0.965(HDO_{space}) \quad \text{Equation 2a}$$

or:

$$TBW = -0.234 + 0.971(^3HHO_{space}) \quad \text{Equation 2b}$$

The proportion of lipid (*%TBL*) and protein (*%TBP*), total body ash (*TBA*, in kg) and total body gross energy (*TBGE*, in Megajoules (MJ)) were calculated according to the same authors as:

$$\%TBL = 105.1 - 1.47(\%TBW) \quad \text{Equation 3}$$

$$\%TBP = 0.42(\%TBW) - 4.75 \quad \text{Equation 4}$$

$$TBA = 0.1 - 0.008(BM) + 0.05(TBW) \quad \text{Equation 5}$$

$$TBGE = 40.8(BM) - 48.5(TBW) - 0.4 \quad \text{Equation 6}$$

where *%TBW* is calculated from total body mass (*BM*) and *TBW*. Calculations of *TBGE* assumed energy densities of 39.5 and 23.5 kJ/g for lipid and protein respectively (Reilly and Fedak, 1990).

We calculated the metabolic rate (expressed as MJ/day) based on changes in total body lipid and protein, assuming the energy densities for lipid and protein cited

above. This method assumes that pups do not obtain energy from external sources during the period of study. Although it is possible that pups may have obtained milk from unknown females, this is extremely unlikely since pups are generally forced out of the harems within 1-2 days after their mothers have departed. Furthermore, during our daily re-sights we never observed any of our study pups interacting with, or even in the vicinity of, other females. It is also theoretically possible that pups may have obtained energy from external sources during their daily excursions into the water towards the end of the fast. However, visual observations of pups in the water suggest that they spend this time either interacting with other pups or floating passively on the surface. Therefore, the assumption that no energy is obtained from external sources during the fast is reasonable.

We also estimated the approximate fractions of available materials that were used while fasting. In the initial calculations we made the same assumptions as in (Fedak et al., 1996) and (McConnell et al., 2002), i.e. we assumed that seals must have a relative lipid content of $> 10\%$ of body mass, and that 70% of the total amount of protein at the beginning of the fast must remain to avoid acute consequences of material loss (Cahill et al., 1979; Cherel et al., 1987; Reilly, 1989). Following (McConnell et al., 2002), we also calculated the approximate days to starvation after the end of the fast, assuming that seals lose body mass and water at similar rates at sea as on land, and again using equations 2 – 5 to estimate body composition and energy content. The assumed critical levels of lipid content and protein loss are very approximate, and are also likely to vary between individuals. We therefore estimated days to starvation using critical values of 50, 60, 70 and 80 % of protein remaining, and for 5, 10, 15 and 20 % relative lipid content.

Results

During the three years of the study, we captured and weighed 310 seals at weaning, and 249 of these were weighed again at departure. From these, we obtained at least 3 sequential measurements of mass from 191 individuals, and data on body composition within 2 days after weaning and within 4-5 days before departure from 67 individuals.

Overall mass changes

The data for mass and duration of males and females broken down by year for the cohorts that were sampled along with data for the entire population are presented in Table 1.

Year	Females			Males			Two-way ANOVA		
	Mean	SD	N	Mean	SD	N	Sex	Year	Interaction
Weaning mass, (entire cohort)	1998	115.88	28.5	560	122.21	28.75	567		
	1999	117.07	26.46	495	122.89	27.17	509	p<0.0001	
(kg)	2000	114.88	26.7	533	119.68	28.87	500		
Weaning mass (kg)	1998	117.83	23.00	46	126.79	26.32	34		
	1999	117.28	30.67	36	124.31	28.74	36		
	2000	142.09	31.82	53	126.25	41.93	44	p=0.0039 (both)	p=0.0145
Departure mass (kg)	1998	88.37	18.96	.	95.18	21.39	.		
	1999	80.83	20.79	.	89.00	20.56	.		
	2000	103.68	24.58	.	92.11	29.08	.	p=0.0009 (1998)	p=0.0074
Fast duration (days)	1998	35.89	9.03	.	36.09	9.40	.		
	1999	42.47	9.14	.	40.72	12.71	.		
	2000	41.55	11.49	.	39.43	12.82	.	p=0.0026 (both)	
Mass loss (kg)	1998	29.46	7.66	.	31.62	9.14	.		
	1999	36.44	12.62	.	35.31	12.77	.		
	2000	38.42	13.20	.	34.14	16.64	.	p=0.0013 (both)	
Daily mass loss (kg/day)	1998	0.84	0.13	.	0.90	0.18	.		
	1999	0.85	0.15	.	0.88	0.17	.		
	2000	0.92	0.17	.	0.84	0.25	.		

Table 1. Mass and mass changes during the post-weaning fast for 202 Southern elephant seals at Macquarie Island, captured at weaning and departure. Weaning masses from the entire weighed cohorts in the three years of study have been included for comparison.

Differences between our sample and the entire population reflect the sampling strategy that aimed to maximise variation in the traits of interest. Weaning mass for all study animals ranged between 62 and 207 kg (124.7 ± 33.6 kg). The duration of the post-weaning fast ranged from 14 to 61 days (38.1 ± 10.8 days), and during this period pups lost 6 to 68 kg (33.1 ± 11.6 kg), representing 27.0 ± 6.1 % of their weaning mass. The total mass lost was positively related to mass at weaning ($ML = -3.25 + 0.30(BM_W)$, $F_{1,246} = 335.4$, $p < 0.0001$, $r^2 = 0.57$, where ML and BM_W denotes total mass loss and weaning body mass respectively), and also to the duration of the fast ($ML = -3.93 + 0.98(DUR_F)$, $F_{1,246} = 768.9$, $p < 0.001$, $r^2 = 0.76$). When these two covariates were included in a linear model along with pup gender and year of study, there was no difference in mass loss between males and females, but there was a small but significant effect of year (Table 2).

	Df	Sum of Squares	Mean Squares	F-ratio	Variance explained (%)	p
Weaning mass	1	22471	22471	1388.51	58.58	<0.0001
Fast duration	1	11265.9	11265.9	696.13	29.37	<0.0001
Year effect	2	1263.5	631.8	39.04	1.65	<0.0001
Gender effect	1	36.9	36.9	2.28	0.1	0.132
Residual error	42	3916.4	16.2		10.3	

Table 2. ANOVA table of the influence of individual explanatory variables and factors in a linear model with total mass loss as the response variable.

This year effect was caused by a slightly higher total mass loss in 1999 and 2000 compared to 1998. The daily rate of mass loss ranged from 0.31 to 1.57 kg/day (0.86 ± 0.17 kg/day), and this rate also increased with weaning mass ($ML_D = 0.40 +$

$0.004(BM_W)$, $F_{1,246} = 224.8$, $p < 0.001$, $r^2 = 0.74$, where ML_D denotes the daily rate of mass loss in kg and BM_W denotes weaning mass, Figure 1A).

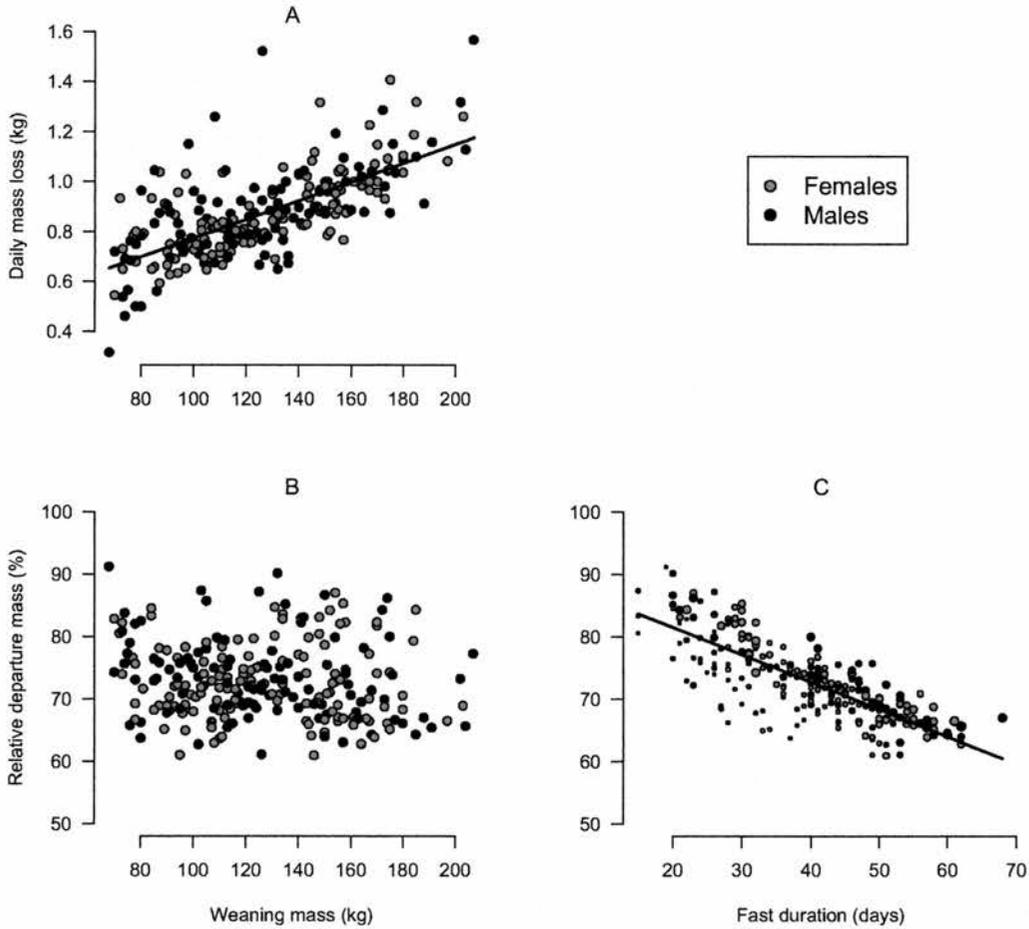


Figure 1. Relationships between weaning mass and A: rate of mass loss, and B: relative departure mass (expressed as percent of weaning mass), and C: relationship between the duration of the post-weaning fast and the relative departure mass. In Figure 1C, the points have been scaled by weaning mass to illustrate the influence of weaning mass on the relative departure mass for any given fast duration.

The slope of this relationship did not vary significantly between years (ANCOVA, $F_{2,244} = 0.64$, $p = 0.52$) or between males and females (ANCOVA, $F_{2,246} = 0.02$, $p = 0.88$), nor was there a significant interaction between year and sex (Two-way ANCOVA, $F_{2,242} = 2.52$, $p = 0.08$). The intercept was significantly greater than zero

($t_{1,146} = 12.14, p < 0.0001$), suggesting that ML_D was not directly proportional to weaning mass, but rather that smaller seals had a higher mass-specific ML_D .

Departure mass ranged from 50 to 160 kg (92.2 ± 23.9 kg), representing on average 73.0 ± 6.15 % of weaning mass, and this percentage was not related to weaning mass ($DM_R = 75.82 - 0.022(BM_W), F_{1,246} = 2.97, p = 0.08, r^2 = 0.012$, where DM_R denotes relative mass at departure in percent, see also Figure 1B). Again, males were slightly heavier at departure in 1998 and 1999 ($t_{66} = 1.47, p = 0.0724$ in 1998 and $t_{70} = 1.67, p = 0.0491$ and 1999 respectively), while females were significantly heavier in 2000 ($t_{84.6} = 2.08, p = 0.0198$), resulting in a significant interaction between year and sex (Two-way ANOVA, $F_{2,243} = 5.01; p = 0.0074$, Table 1). The relative mass at departure was strongly negatively correlated with the duration of the fast ($DM_R = 90.20 - 0.44(DUR_F), F_{1,246} = 389.9, p < 0.0001, r^2 = 0.61$, Figure 1C). Furthermore, the residuals of this regression were positively related with mass at weaning (Figure 1C), so that for any given fast duration pups with a higher weaning mass had a higher relative departure mass. This is also consistent with the fact that both covariates (weaning mass and fast duration) were significant in the linear model of total mass loss (Table 2).

Sequential mass changes

We obtained data on sequential mass loss throughout the fast for 191 pups that were captured at least three times during the fast. Although the mass loss was broadly linear throughout this period (Figure 2), there was nevertheless evidence of significant changes with time.

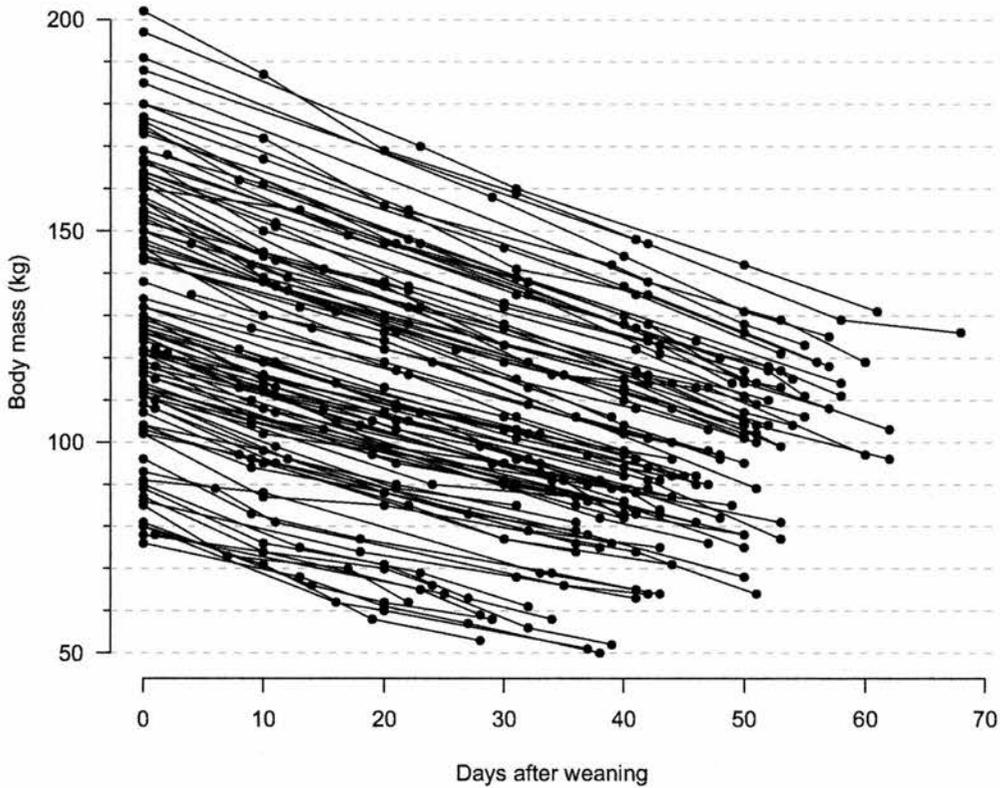


Figure 2. Sequential changes in mass of pups weighed at least three times during the post-weaning fast.

Both the absolute and mass-specific rates of mass loss changed in a non-linear fashion over the fast, and were also positively related to weaning mass (Figure 3 A & B, Table 3 A & B). The absolute rate decreased over the first 10-20 days, and again increased for fast durations > 35-40 days (Figure 3 A). When expressed in mass-specific terms, the early decrease was less pronounced, while there was again a relatively distinct increase for fast durations >35-40 days. Linear mixed effects models including weaning mass and 2nd and/or 3rd degree polynomials of number of days after weaning provided significantly better fits than models that did not include these parameters, while not being penalised by the number of parameters (Table 3). The most parsimonious model for absolute mass loss rate included a 3rd degree polynomial: $DL_{Abs} = 0.42 + 0.004(BM_W) - 1.02(Day) + 1.45(Day)^2 - 0.60(Day)^3$, $AIC_{ML} = 154.06$, $logLik = -70.03$, $AIC_W = 0.74$, where DL_{Abs} is the absolute mass loss

rate, BM_W denotes weaning mass, Day is the number of days after weaning, and AIC_W is the Akaike weight of the model, see also Table 3A). The most parsimonious model for the mass-specific rate of mass loss (i.e. the rate over each interval as a function of the average mass during the interval) included a 2nd degree polynomial: $DL_{Rel} = 13.93 - 0.04(BM_W) + 8.17(Day) + 13.75(Day)^2$, $AIC_{ML} = 1856.1$, $logLik = -922.04$, $AIC_W = 0.59$, where DL_{Rel} is the relative mass loss rate, Table 3B). The inclusion of a 3rd degree polynomial did not improve the fit of this model (ANOVA, Likelihood ratio = 1.29, $p = 0.255$), and the extra parameter gave this model a lower AIC weight than the model only including a 2nd degree polynomial (Table 3 B).

Response	Model	logLik	nPar	AIC	dAIC	AICw
A. Absolute mass loss rate	WMass + poly(day, 3)	-70.03	5	154.1	0	0.745
	WMass + poly(day, 2)	-72.10	4	156.2	2.145	0.255
	WMass + day	-83.41	3	176.8	22.763	0
	Wmass	-89.24	2	186.5	32.425	0
	poly(day, 3)	-95.20	4	202.4	48.340	0
B. Mass-specific mass loss rate	WMass + poly(day, 2)	-922.05	4	1856.1	0	0.587
	WMass + poly(day, 3)	-921.40	5	1856.8	0.706	0.413
	WMass + day	-930.91	3	1871.8	15.737	0
	Wmass	-933.28	2	1874.6	18.475	0
	poly(day, 3)	-943.35	4	1898.7	42.599	0

Table 3. Comparison of linear mixed effects models of sequential rates of absolute (Table 3 A) and mass-specific (Table 3 B) rates of mass loss throughout the post-weaning fast of Southern elephant seals at Macquarie Island. "Wmass" represents weaning mass and "Day" denotes the day after weaning of the midpoint between two consecutive measurements of body mass loss. The "poly" argument represents the inclusion of polynomial parameters (2nd or 3rd degree) to model the curvilinearity in the relationship. "logLik" refers to the log-likelihood value of the model, nPar indicate the number of parameters, AIC refers to Akaike's Information Criterion, dAIC is the difference in AIC between each model and the best model, and AICw is the relative weight of evidence in support of each model.

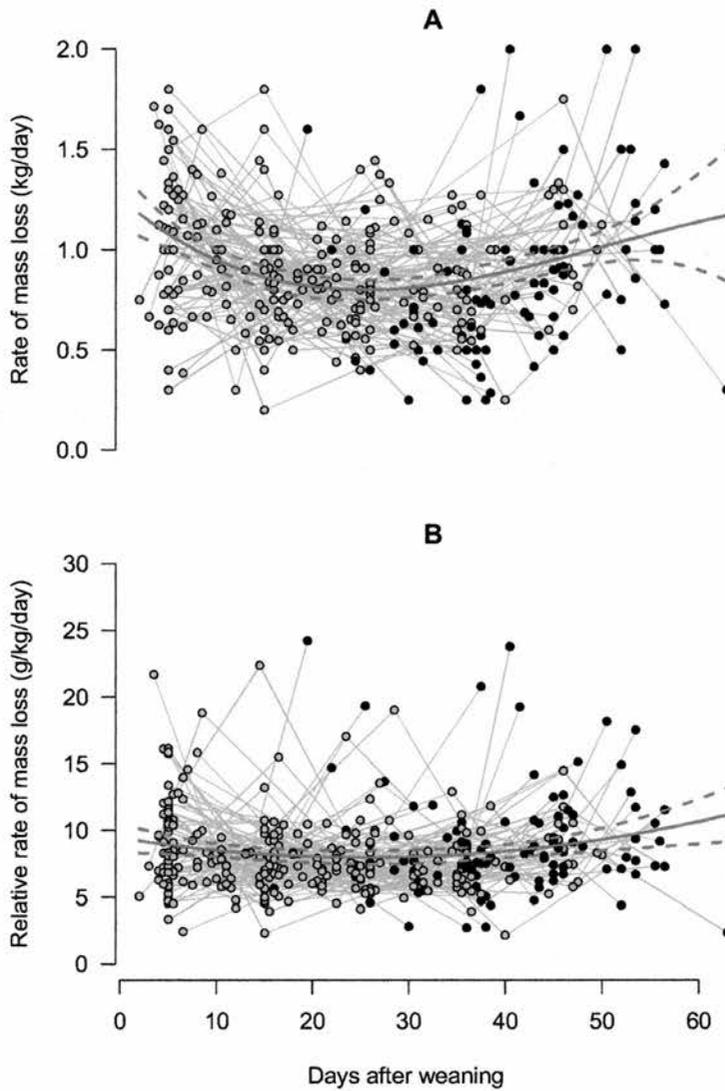


Figure 3. Sequential rates of mass loss during the post-weaning fast. Each data point represents the absolute (A) and mass-specific (B) rate of mass loss for an individual between two consecutive captures. The mass-specific rate was calculated based on the average mass of an individual over a given interval (see text). The solid red curves represent 3rd (Fig. 3 A) and 2nd (Fig. 3 B) degree polynomial regression lines based on linear mixed effects models (see Table 3). The broken lines represent the 95% confidence interval of the fitted curves. Grey filled circles represent sequential measurements, and black filled circles represent the final measurement for each individual.

Summary of body composition measures

In this section we present summary and group statistics for body composition and energy measurements of the sampled animals at weaning and towards the end of the post-weaning fast.

Weaning

We obtained data on body composition at weaning for 101 pups and at departure for 95 pups. Of these, 67 pups were measured at both weaning and departure, allowing us to examine longitudinal changes over the fast. Data for these 67 pups are presented in Table 4. For the 101 pups examined at weaning, lipid content ranged from 25.3 to 98.3 kg (56.8 ± 14.7 kg), representing 30.1 – 54.9 % (44.9 ± 4.5 %) of their body mass. This proportion increased slightly with body mass ($\%TBL_W = 40.28 + 0.037(BM_W)$, $F_{1,99} = 5.29$, $r^2 = 0.041$, $p = 0.023$), and this relationship did not differ significantly between the sexes ($T_{1,97} = 1.24$, $p = 0.219$). Protein content at weaning ranged from 8.9 to 26.3 kg (15.6 ± 3.4 kg), representing 9.6 – 16.7 % (12.4 ± 1.3 %) of total body mass. The total energy content (TBGE) varied from 1312 to 4511 MJ (2646 ± 644 MJ), representing an energy density of 16.1 to 24.2 MJ/kg (20.9 ± 1.5 MJ/kg). There were no significant differences between the sexes or years of study (ANCOVA_{Sex*Year}, energy content: $F_{5,95} = 0.22$, $p = 0.95$; energy density: $F_{5,95} = 0.16$, $p = 0.98$).

	Year:1998						Year:1999						Year:2000						All seals		
	Females		Males		N=12		Females		Males		N=10		Females		Males		N=12		N=67		
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	
WEANING																					
Lactation duration	23	2.83	24.17	2.79	24.27	2.57	23.9	2.38	24.62	2.81	24.6	2.67	24.17	2.62	24.17	2.62	24.17	2.62	24.17	2.62	
Day of first capture	0.29	0.49	0.33	0.65	0.27	0.47	0.4	0.84	0	0	0.58	1.24	0.3	0.72	0.3	0.72	0.3	0.72	0.3	0.72	
Weaning mass	127.43	19.18	128.08	33.27	129.27	32.65	127.1	27.34	134.93	33.32	123.92	12.93	128.85	27.54	128.85	27.54	128.85	27.54	128.85	27.54	
Lipid %	46.24	3.95	45.53	4.8	47.66	5.11	46.36	5.49	45.3	2.13	45.39	1.94	46	3.95	46	3.95	46	3.95	46	3.95	
Protein %	12.07	1.13	12.27	1.37	11.66	1.46	12.03	1.57	12.34	0.61	12.31	0.55	12.14	1.13	12.14	1.13	12.14	1.13	12.14	1.13	
Total lipid	59.29	12.66	58.89	18.87	62.09	18.74	59.59	16.9	61.1	15.29	56.32	7.05	59.6	15.08	59.6	15.08	59.6	15.08	59.6	15.08	
Total protein	15.27	1.91	15.55	3.73	14.94	3.5	15.1	2.77	16.65	4.21	15.23	1.53	15.54	3.18	15.54	3.18	15.54	3.18	15.54	3.18	
Total body gross energy	2736	529.6	2726.93	818.02	2839.91	811.65	2744.2	718.53	2841.84	705.8	2616.72	308.27	2754.99	659.8	2754.99	659.8	2754.99	659.8	2754.99	659.8	
DEPARTURE																					
Age at departure	55.71	9.01	57.58	10.11	70.55	9.07	71.1	6.44	71	8.95	70.7	3.13	66.63	10.2	66.63	10.2	66.63	10.2	66.63	10.2	
Fast duration	33	7.79	33.75	9.27	46.55	8.84	47.6	8.06	46.64	8.48	46	4.09	42.86	9.74	42.86	9.74	42.86	9.74	42.86	9.74	
Departure mass	99	18.61	97.17	26.79	85.82	19.71	86.1	18.24	94.87	20.04	86.75	9.58	91.46	19.6	91.46	19.6	91.46	19.6	91.46	19.6	
Lipid %	44.22	2.54	43	4.19	42.19	1.78	40.4	1.72	43.02	2.24	41.1	3.28	42.27	2.94	42.27	2.94	42.27	2.94	42.27	2.94	
Protein %	12.64	0.73	12.99	1.2	13.23	0.51	13.74	0.49	12.99	0.64	13.54	0.94	13.2	0.84	13.2	0.84	13.2	0.84	13.2	0.84	
Total lipid	44.05	9.79	41.82	12.71	36.36	9.22	34.88	7.98	40.77	8.59	35.68	5.24	38.79	9.38	38.79	9.38	38.79	9.38	38.79	9.38	
Total protein	12.44	2.03	12.61	3.5	11.31	2.41	11.8	2.39	12.33	2.81	11.73	1.48	12.04	2.52	12.04	2.52	12.04	2.52	12.04	2.52	
Total body gross energy	2059.28	435.61	1974.49	577.51	1724.74	423.96	1677.56	373.83	1925.62	402.35	1708.12	223.41	1839.38	425.69	1839.38	425.69	1839.38	425.69	1839.38	425.69	
CHANGES																					
Mass change	-28.43	2.99	-30.92	9.11	-43.45	14.4	-41	11.39	-40.07	14.57	-37.17	4.3	-37.39	11.74	-37.39	11.74	-37.39	11.74	-37.39	11.74	
Lipid change	-15.23	6.67	-17.07	7.59	-25.73	11.05	-24.72	10.46	-20.33	8.11	-20.64	4.07	-20.81	8.72	-20.81	8.72	-20.81	8.72	-20.81	8.72	
Protein change	-2.83	1.57	-2.94	1.52	-3.63	1.72	-3.3	1.15	-4.32	1.76	-3.5	0.97	-3.5	1.52	-3.5	1.52	-3.5	1.52	-3.5	1.52	
Percent lipid change	-2.02	4.72	-2.53	3.79	-5.47	4.89	-5.96	4.49	-2.28	2.74	-4.29	3.22	-3.73	4.06	-3.73	4.06	-3.73	4.06	-3.73	4.06	
Percent protein change	0.58	1.35	0.72	1.08	1.56	1.4	1.7	1.28	0.65	0.78	1.23	0.92	1.07	1.16	1.07	1.16	1.07	1.16	1.07	1.16	
Energy change	-676.72	231.45	-752.44	295.62	-1115.17	444.38	-1066.64	410.42	-916.21	351.97	-908.61	152.46	-915.61	351.39	-915.61	351.39	-915.61	351.39	-915.61	351.39	
Daily lipid change	-0.49	0.23	-0.52	0.21	-0.56	0.21	-0.5	0.16	-0.44	0.11	-0.45	0.08	-0.49	0.17	-0.49	0.17	-0.49	0.17	-0.49	0.17	
Daily protein change	-0.09	0.05	-0.09	0.05	-0.08	0.03	-0.07	0.03	-0.09	0.03	-0.08	0.02	-0.08	0.03	-0.08	0.03	-0.08	0.03	-0.08	0.03	
Daily energy expenditure	21.57	8.35	22.85	8.25	24.04	7.85	21.87	5.87	19.92	4.54	20.01	2.91	21.62	6.34	21.62	6.34	21.62	6.34	21.62	6.34	
Total energy from lipid	601.74	263.33	674.16	299.86	1016.49	436.58	976.39	413.13	803.14	320.32	815.3	160.9	822.06	344.45	822.06	344.45	822.06	344.45	822.06	344.45	
Total energy from protein	66.59	36.9	69.06	35.69	85.35	40.42	77.59	26.93	101.5	41.31	82.2	22.7	82.37	35.74	82.37	35.74	82.37	35.74	82.37	35.74	
% energy from lipid	86.65	8.59	87.75	6.66	89.64	6.73	89.62	6.68	87.11	4.38	89.32	3.52	88.36	5.88	88.36	5.88	88.36	5.88	88.36	5.88	

Table 4. Changes in mass and body composition during the post-weaning fast. Energy content refers to total body gross energy (TBGE), and was calculated) using the equations derived for grey seals by (Reilly and Fedak, 1990), assuming energy densities of 39.5 kJ/g and 23.5 kJ/g for lipid and protein respectively Daily energy expenditure refers to the daily change in TBGE.

Departure

For the 95 pups examined towards the end of the fast, total body lipid ranged from 24.0 – 72.4 kg (38.4 ± 9.3 kg), representing 30.5 – 50.6 % (41.8 ± 3.5 %) of body mass. Females had a slightly but significantly higher relative lipid content than males (42.7 ± 3.1 % and 41.0 ± 3.6 % for females and males respectively, $t_{92.9} = 2.40$, $p = 0.018$). Again, this proportion increased with body mass ($\%TBL_D = 37.13 + 0.051(BM_D)$, $F_{1,94} = 7.42$, $r^2 = 0.063$, $p = 0.008$), but the slope was not significantly different for males and females ($T_{1,92} = -1.55$, $p = 0.124$). At the end of the fast, the average relative lipid content was ~ 3 % lower ($T_{187.82} = 5.44$, $p < 0.0001$), while the variance around this mean was more than 50% less ($F_{100,95} = 1.65$, $p = 0.014$) compared to weaning (Figure 4).

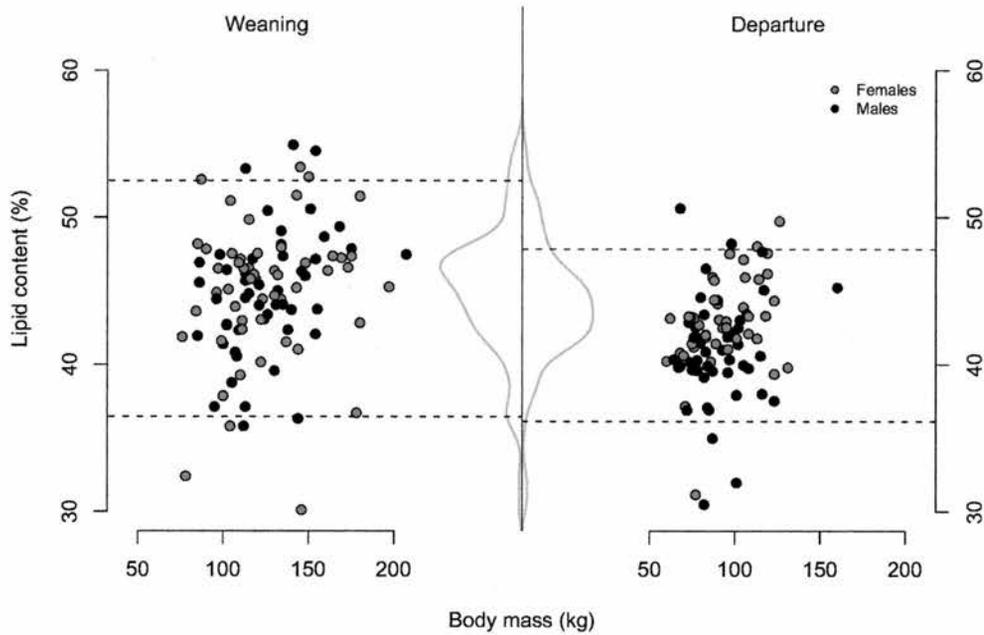


Figure 4. Relationships between body mass and relative lipid content at weaning and departure. Each point represents one individual, the points in the left- and right-hand plot represent all pups for which body composition was analysed at weaning and departure respectively. Most pups were measured at both these times, but some points in either plot represents pups that were only measured at that particular time. The vertical grey curves represent kernel density distributions of lipid content (calculated using a bandwidth of 1 percent units) corresponding to weaning and departure (left- and right-hand curve respectively). The horizontal broken lines represents the range defined by a cumulative density d of $5 \leq d \leq 95$ % of the total cumulative density.

While the lower limit of the range in lipid content did not vary between the two captures, the upper limit was significantly lower at departure compared to weaning (Figure 4), and pups at the lower end of lipid contents tend to maintain their relative body composition, while fatter pups decrease their relative lipid content throughout the fasting period. The total energy content of these 95 pups ranged from 1164 to 3368 MJ (1825 ± 413.2 MJ), representing an energy density of 16.2 to 22.8 MJ/kg (19.9 ± 1.1 MJ/kg). There were no significant differences between the three years (ANCOVA_{Year}, energy content: $F_{2,93} = 1.92$, $p = 0.15$; energy density: $F_{2,93} = 0.43$, $p =$

0.65). While there were no significant differences in absolute energy content at departure between males and females (ANOVA_{Sex}, energy content: $F_{1,94} = 0.82, p = 0.36$), females had a significantly higher energy density at departure compared to males (ANOVA_{Sex}, energy density: $F_{1,94} = 5.72, p = 0.019$).

Energy expenditure and material allocation

Among the 67 seals that were captured at weaning and again at departure total mass loss ranged from 18.0 to 68.0 kg (37.4 ± 11.7 kg). Of this lipid constituted 31.6 - 88.6 % ($54.7 \pm 13.5\%$), protein 0.0 - 16.2 % (9.6 ± 3.9 %), and water 11.2 - 50.0 % (34.3 ± 9.2 %). The total energy loss was 306.6 to 1688.0 MJ (915.6 ± 351.4 MJ), representing 16.0 to 47.1 % (32.6 ± 7.7 %) of total energy at the end of lactation. The daily energy expenditure (*DEE*) ranged from 9.8 to 38.1 MJ/day (21.5 ± 6.4 MJ/day). This was positively related to body mass according to the equation:

$$\log_{10}DEE = -0.53 + 0.91 \log_{10}(BM_{Av})$$

or transformed:

$$DEE = 0.29 + BM_{Av}^{0.91}$$

where BM_{Av} is the average of weaning and pre-departure mass for each individual. The regression statistics for the logarithmic function were: $F_{1,65} = 37.57, r^2 = 0.36, p < 0.0001$. As expected, the energy expended during the fast was derived primarily from the oxidation of lipid, although the relative energetic contribution of lipid (E_{lipid}) varied considerably between individuals, from ~75 to 99 % (88.4 ± 5.9 %). While

E_{lipid} was high and relatively constant among individuals with a relatively higher lipid content at weaning, individuals that started off leaner had a lower and more variable E_{lipid} (Figure 5).

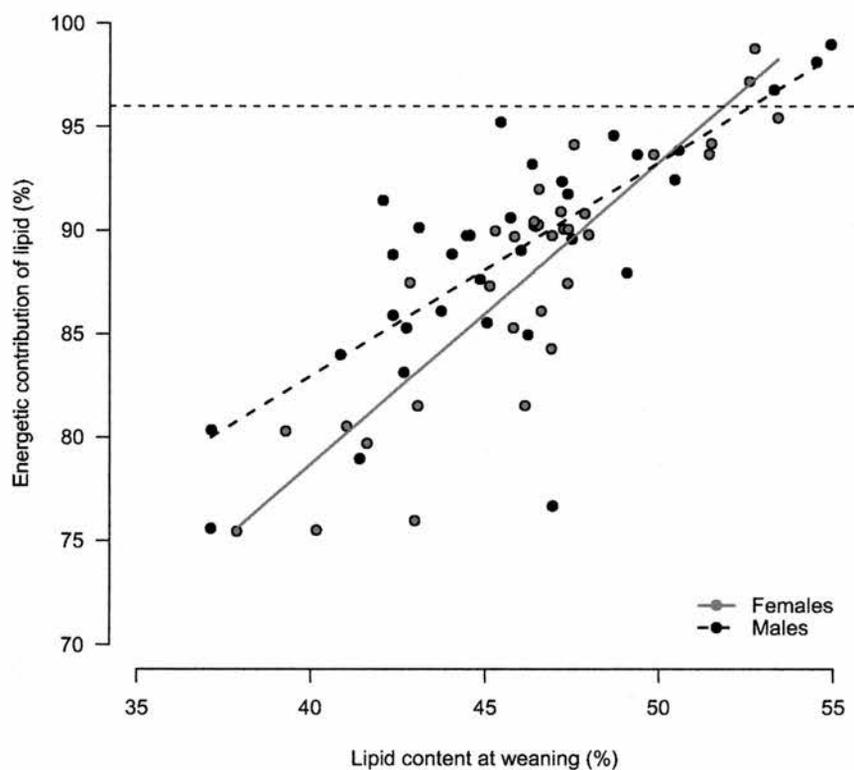


Figure 5. The energetic contribution of lipid as a function of relative lipid content at weaning. The horizontal broken line is a reference representing a relative contribution of 96 %.

Despite the greater variance among leaner individuals, the relationship between initial lipid content ($\%TBL_w$) and E_{lipid} was highly significant for all seals combined:

$$E_{lipid}(\%) = 32.97 + 1.20(\%TBL_w), F_{(1,65)} = 123, r^2 = 0.65, p < 0.001$$

The average E_{lipid} was not significantly different between males and females ($t_{64.1} = 0.69, p = 0.49$). However, the slopes for each sex treated separately were significantly different (ANCOVA, interaction term: $F_{1,63} = 4.14, p = 0.046$, Figure 5). The equations for each sex were:

$$\text{Females: } E_{lipid}(\%) = 20.4 + 1.46(\%TBL_W), F_{(1,31)} = 117.2, r^2 = 0.78, p < 0.001$$

$$\text{Males: } E_{lipid}(\%) = 41.7 + 1.03(\%TBL_W), F_{(1,32)} = 44.03, r^2 = 0.56, p < 0.001$$

While the slope for males was not significantly different from 1 ($t_{1,32} = 0.20, p = 0.84$), the slope for females was significantly greater than 1 ($t_{1,31} = 3.39, p = 0.002$).

While males and females with a high initial relative lipid content had a similar E_{lipid} , lean females had a lower E_{lipid} compared to lean males (Figure 5). As a result of these differences, the relationship between relative lipid content at weaning and departure was very different between male and female pups (Figure 6). While there was no relationship between $\%TBL_W$ and $\%TBL_D$ for females ($\%TBL_D = 40.15 + 0.061(\%TBL_W), F_{1,31} = 0.34, r^2 = 0.01, p = 0.565$), this relationship was significant for males ($\%TBL_D = 24.28 + 0.38(\%TBL_W), F_{1,32} = 8.80, r^2 = 0.21, p = 0.006$). But these are very scattered relationships. If you superimpose one on the other I would be struck more by their similarity than their differences.

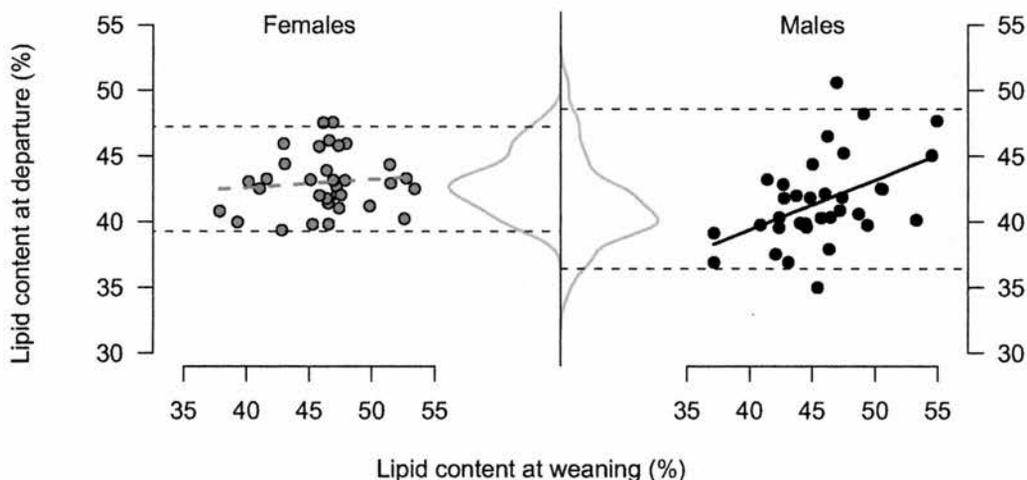


Figure 6. Relationships between relative lipid content at weaning and departure for males and females respectively. The vertical grey curves represent kernel density distributions of lipid content at departure (calculated using a bandwidth of 1 percent units) for males and females (left- and right-hand curve respectively). The horizontal broken lines represents the range defined by a cumulative density d of $5 \leq d \leq 95$ % of the total cumulative density.

Fractional use of available body components

The variations in E_{lipid} and $E_{protein}$ resulted in large individual differences in the fractional use of body components assumed to be available as a source of energy (Figure 7). The fraction of available protein used (P_{frac}) increased asymptotically with increasing $E_{protein}$ (asymptotic regression: $P_{frac} = 1.02(1 - \exp(-\exp(-1.84) E_{protein}))$, where 1.02 represents the upper asymptote (in fractions) and -1.84 represents the rate constant), Residual $S.E._{.65} = 0.13$), while the fraction of available lipid used (L_{frac}) decreased linearly with increasing $E_{protein}$ ($L_{frac} = 0.53 - 0.012(E_{protein})$, $F_{1,65} = 69.6$, $r^2 = 0.51$, $p < 0.0001$).

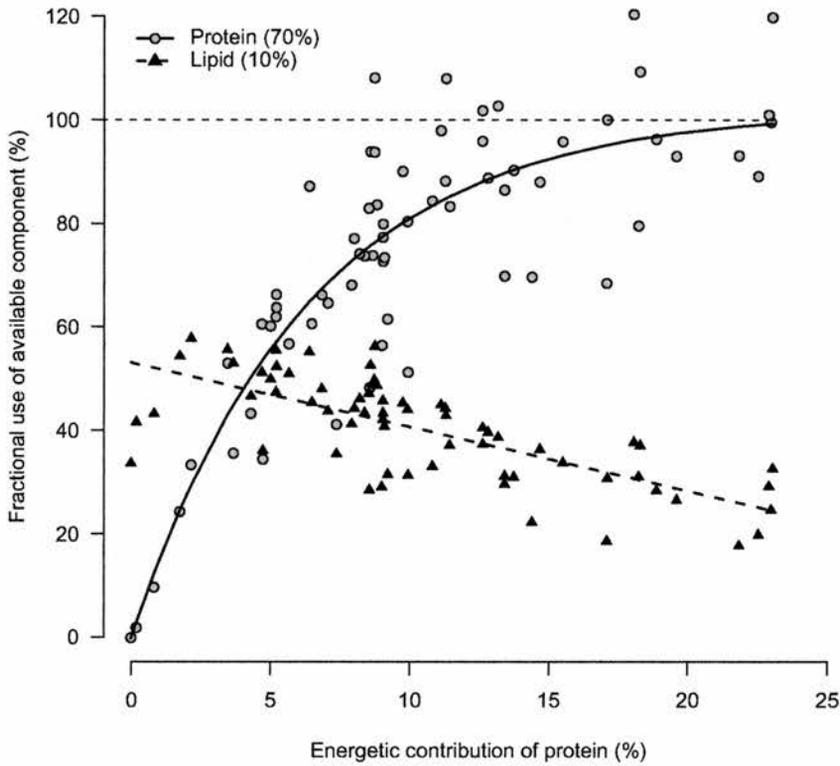


Figure 7. The fractional use of a particular component (lipid and protein) relative to the amount available as a source of energy, plotted against the relative energetic contribution of protein to the overall energy expenditure. The amount of available protein was calculated assuming that 70% of body protein must remain to avoid acute consequences of material loss, and that a relative lipid content of 10 % before acute loss of structural lipid and/or thermal insulation (Cahill et al., 1979; Cherel et al., 1987; Reilly, 1989). The curve for fractional protein use represents a nonlinear asymptotic regression model through the origin, of the form: $y = A(1 - e^{-e^B x})$, where A is the upper asymptote and B is the natural logarithm of the rate constant (see results for further details).

Estimated days to starvation

When we extended the above analysis to estimate days to starvation using a range of critical values for component use, protein depletion proved the most critical limitation of the two. Figure 8 A shows the effect of varying the critical threshold of the fraction

of the initial amount of protein that must remain to avoid acute effects (P_c) from 80 to 50 % on the number of days until pups in our sample are predicted to have died from acute protein depletion. These predictions were made assuming a critical lipid content (L_c) of 10 % (i.e. at least 10 % of total body mass must be in the form of lipid). While the total range of days did not vary substantially, the distribution varied dramatically (Table 5). Assuming a critical value of 80 % protein remaining (P_{c80}), 75 % of our pups were estimated to have died after only 5 days. The corresponding number of days at P_{c70} , P_{c60} and P_{c50} were 26, 45 and 59 days respectively. The proportion of animals dying from protein depletion decreased successively from 92.5 % at P_{c80} to 73.1 % at P_{c50} . As a result of the high proportion of animals predicted to die from protein rather than lipid depletion irrespective of which P_c value was used, the estimated days to starvation was insensitive to changes in L_c over the range 5 – 20 % (Figure 8 B).

Critical protein	Summary of estimated days to starvation						Number of seals dying from:	
	Min	25%	Median	Mean	75%	Max	Lipid depletion	Protein depletion
80%	0	0	0	6.7	5	71	5	62
70%	0	4	12	17.9	26	71	6	61
60%	5	19.5	29	33.4	45.5	77	10	57
50%	18	36	47	46.4	59	77	18	49

Table 5. Summary of the effects of using critical thresholds of 50, 60, 70 and 80 % for the fraction of initial protein content that must remain in order for seals to avoid acute loss of lean tissue.

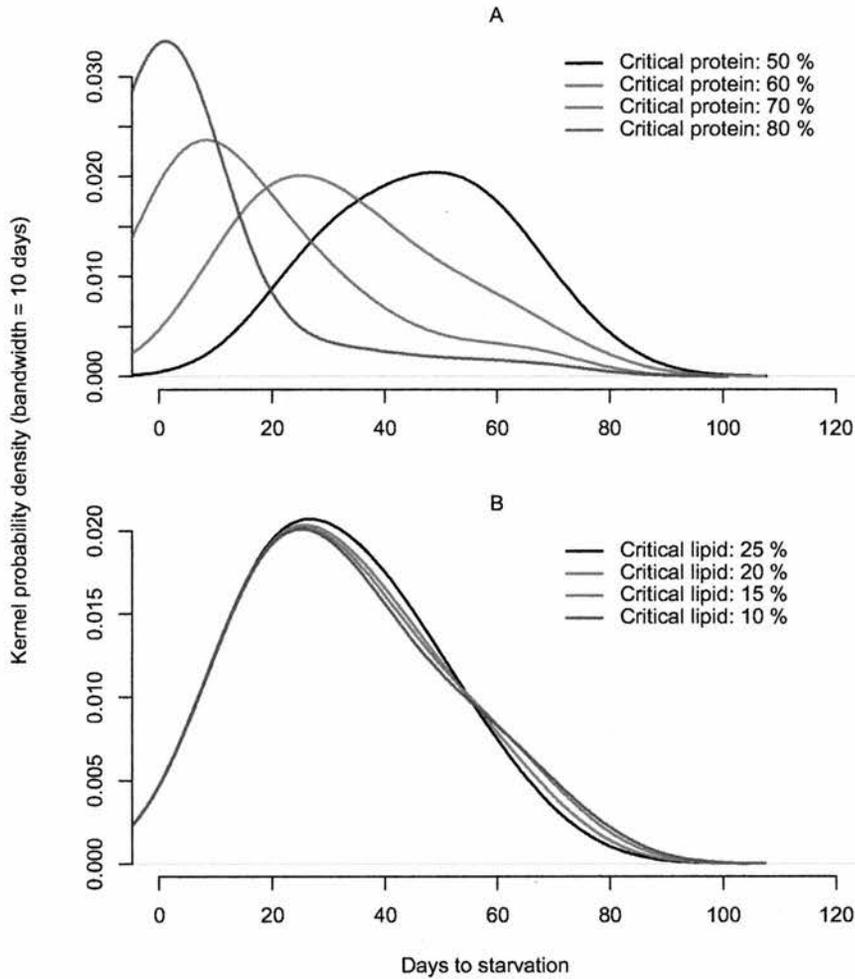


Figure 8. Kernel density plots of the number of days to starvation after the second capture for the 67 study seals. The number of days was estimated by extrapolating the rate of mass and water loss from the post-weaning fast, and then calculating the body composition based on equations 2 – 5 (taken from (Reilly and Fedak, 1990)). A) The four curves represent probability distributions of days to starvation assuming critical thresholds of 50, 60, 70 and 80 % protein remaining to avoid acute loss of lean tissue, assuming a threshold for relative lipid content of 10 % of body mass. B) The curves represent probability distributions of days to starvation assuming critical thresholds of 10, 15, 20 and 25 % relative lipid content to avoid the loss of structural lipid and/or thermal insulation.

Discussion

We have shown that it is not only the size of a pup at weaning that is important in shaping the patterns of resource use and energy expenditure while fasting, but that factors relating to gender and initial body composition were also important. We have demonstrated that pups at the top end of initial relative lipid content rely almost exclusively on lipids to supply energy during the post-weaning fast, irrespective of their gender. In contrast, among pups with initially lower lipid contents, males tend to rely to a greater extent on lipid compared to females. We have also expanded the ideas developed in (McConnell et al., 2002) regarding the ways in which resource allocation and energy usage of pups while fasting on land may influence the probability of them surviving the initial critical period at sea before they find food. This analysis (although based on several approximations and assumptions) suggest that, despite the fact that our seals (like phocids in general) derive most of their energy while fasting from lipid, protein depletion may still be much more critical for their early at-sea survival.

Overall mass changes

As expected, there was a significant positive relationship between the mass at weaning and the rate of mass loss (Fig 1A), and the general relationship between rate of mass loss and mass at weaning in this study was similar to that reported from South Georgia by (Arnbom et al., 1993). However, in contrast to the studies from King George Island and Año Nuevo, we also found a significantly greater variation in the rate of mass loss for smaller seals than for larger seals (Figure 9).

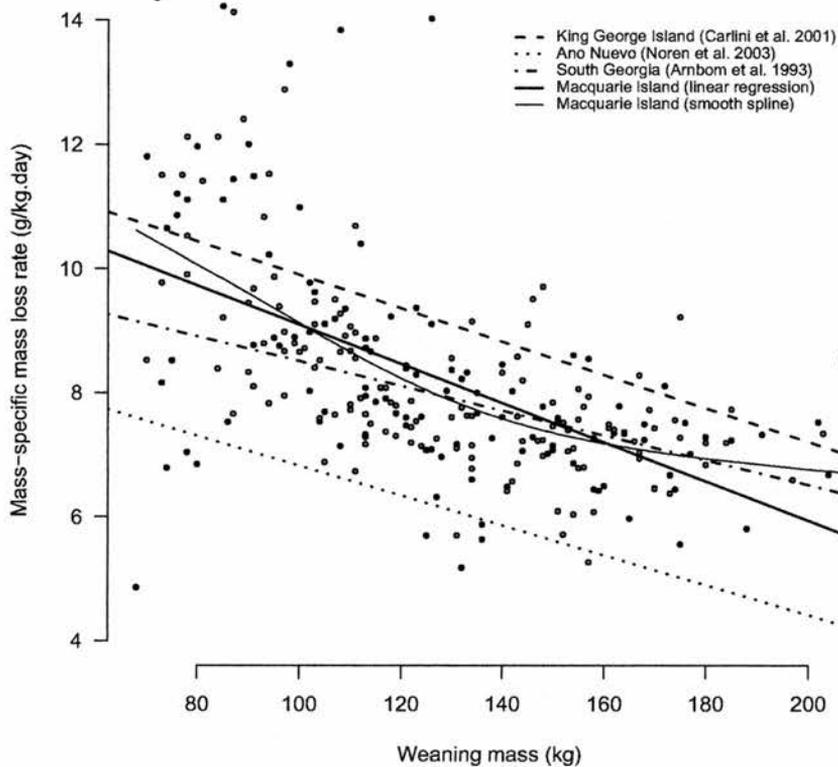


Figure 9. Mass-specific rate of mass loss ($\text{g kg}^{-1} \text{day}^{-1}$), as a function of average body mass during the post-weaning fast (i.e. average of weaning mass and mass at last capture). The three straight lines represent linear regressions for Macquarie Island (i.e. based on the points in the plot), and for Southern elephant seals at King George Island (Carlini et al., 2001) and for Northern E.S. at Año Nuevo (Noren et al., 2003). The curve is a smooth spline function fitted to the points to illustrate the general non-linear trend in the data from Macquarie Island (see text for further details).

This pattern appears to be a result of substantial variations in the rate of mass loss for animals with a weaning mass < 100 kg. The South Georgia study shows a similar pattern, although not as striking as for pups at Macquarie Island. In fact, some of our smallest pups had absolute rates of mass loss of ~ 1 kg/day, similar to some of the largest pups. For a large pup (e.g. 200 kg), this represents a daily mass loss of only ~ 5 $\text{g kg}^{-1} \text{day}^{-1}$ (0.5 % of initial body mass), while for a small pup (e.g. 70 kg) it is almost

be caused by unusually high activities in these smaller pups. However, based on visual observations there is no evidence to suggest a relationship (positive or negative) between activity patterns and body size.

Sequential mass changes

As with previous studies, we found a significant decrease in the absolute rate of mass loss throughout the portion of the fast, and for pups that remained on land for more than about one month, the rate again increased over the last couple of weeks prior to departure (Figure 4A). (Arnbom et al., 1993) found a similar pattern for weaned pups at South Georgia, where the rate of mass loss (absolute and mass-specific) were higher during the first and last 10 days compared to the middle period of the fast. Although this pattern was not as obvious when expressed in mass-specific terms (in particular the decrease over the initial fasting period), the significance of the polynomial terms in the mixed effects models suggests that the changes in mass loss rate are not simply a result of pups becoming gradually smaller. In particular, the fact that the mass-specific rate increased in pups remaining on land for at least 1 month suggests that this extended fasting may be associated with changes in relative use of lipids and protein to supply energy. This increase may suggest that these long-fasting pups may increase their protein catabolism during the later stages, although the changes are not dramatic enough to suggest a sudden switch to stage III fasting. It is therefore unlikely that departure to sea was triggered by increased levels of metabolites such as blood urea nitrogen (BUN) produced by the breakdown of protein (Castellini and Rea, 1992). Therefore, those of our seals that derived a substantial proportion of their energy from the catabolism of protein most likely did so throughout the fast rather than at the end.

Body composition and energy expenditure

There are now a number of published reports on the changes in body composition and energetics of fasting in newly weaned northern (Kretzmann et al., 1993; Noren et al., 2003), southern (Carlini et al., 2001; Carlini et al., 2000) elephant seal and grey seal (Iverson et al., 1993; Reilly, 1991) pups. Although these studies show broad similarities, there are some striking differences, including some within the same species. For instance, while the earlier study by (Kretzmann et al., 1993) found no relationship between total body mass and the proportion of lipid at weaning in northern elephant seal pups, (Noren et al., 2003) found a strong positive relationship, possibly due to a larger sample size and wider range of body size in the more recent study. In the two studies on fasting grey seal pups, (Reilly, 1991) and (Iverson et al., 1993) also found strong positive relationships between mass and relative lipid content at weaning. In contrast, (Carlini et al., 2001) found no such relationship in southern elephant seals on King George Island. In this study, we found no evidence of a strong relationship between mass and relative lipid content at weaning (Fig 1A), and our results therefore support those of (Carlini et al., 2001). Furthermore, (Rea and Costa, 1992) found that the relative lipid content in northern elephant seal pups remained fairly constant throughout the post-weaning fast, while (Noren et al., 2003) reported a slight increase (from ~28 – 43 % at weaning to ~32 – 46 % at departure). In contrast, (Carlini et al., 2001) showed that the relative lipid content of southern elephant seals decreased significantly throughout the fast (from ~37 % at weaning to 34 % at departure). Although our results show a decrease of similar magnitude as that reported by (Carlini et al., 2001), the lipid contents of our pups were overall much higher (~45 % at weaning and ~43 % at departure) compared to pups at King George. This is

somewhat surprising because of the much larger overall body size of pups at King George. The average metabolic rate (MR) in our study (21.5 MJ/day) was similar to that reported by (Carlini et al., 2001), but much higher than that reported for northern elephant seals (Noren et al., 2003). There were also considerable variations between individuals. Our estimates of MR were equivalent to 0.9 – 4.1 (1.9 ± 0.48) times the estimated basal metabolic rate of a terrestrial mammal of the same size (Kleiber, 1975), and 0.6 – 3.3 (1.4 ± 0.36) times the estimated resting metabolic rates calculated using empirical equations derived from measurements on adult grey seals (Pullen, 1988).

Differences between females and males

In contrast to previous studies of body composition and energy metabolism in newly weaned fasting elephant seal pups, this study suggests that there are fundamental differences in the way male and female pups allocate their resources after the end of lactation. These differences appear among smaller pups that presumably received less energy and material from their mothers, and that may have to be more careful with the way they utilise their energy reserves. Leaner males derived a greater proportion of their energy from stored lipid compared to females of similar body compositions (Figure 5). As a result, the percent lipid at departure is not significantly different in initially leaner females compared to that of fatter females, while the percent lipid at departure of initially leaner males is significantly lower than that of fatter males and females (Figure 6). Furthermore, even within each sex the relative reliance on lipid catabolism is more variable among leaner individuals. This suggests that, regardless of sex or other individual characteristics, fat animals are able to maximise their reliance on lipid in order to spare their protein reserves, without seriously depleting their lipid

that derived most of their energy from lipid catabolism during the fast may be retained as much as ~ 50 – 60 % of their available lipid at the end of the fast (Figure 7). The common assumption that 70 % of body protein must remain at the end of the fast to avoid acute effects of lean tissue loss (Cahill et al., 1979; Cherel et al., 1987; Reilly, 1989), see also (Fedak et al., 1996; McConnell et al., 2002), therefore may be too conservative. Previous studies using movement patterns (McConnell et al., 2002), travel rates (Hindell et al., 1999; McConnell et al., 2002), and dive indices of changes in relative body composition (Biuw et al., 2003) suggest that the majority of pups spend at least 25-30 days in transit (Phase 1) before they reach their foraging grounds. Using the 70 % critical protein level, and assuming similar energy expenditures at sea and on land (see discussion in (McConnell et al., 2002)), less than half of the pups would be expected to survive more than about 2 weeks at sea, and only ~ 25 % would survive until the end of Phase 1 (Figure 8 and Table 5). If we instead assumed that seals can expend ~ 40 % of their initial body protein before risking acute tissue loss, ~ 75 % of our seals would be expected to survive until around day 20, and half of them would still be alive after one month. If previously suggested indices of foraging are true, this would dramatically increase the probability of seals surviving until they have reached feeding grounds. These survival estimates may appear high considering the large size of elephant seal pups. However, the most recent estimate of first year survival at Macquarie Island (based on more than 4000 pups individually marked over 5 years and re-sighted over a period of eight years) is more than 70% (McMahon et al., 2003), so our estimates appear to be reasonable.

As discussed in (McConnell et al., 2002), these calculations are based on several assumptions and extrapolations, such as similar rates of energy and material use of

- Associated Apnea in Northern Elephant Seals. *American Journal of Physiology-Regulatory Integrative and Comparative Physiology*, 36:R1294-R1301.
- Cherel, Y., Y. P. Robin, and Y. LeMaho. 1987. Physiology and biochemistry of longterm fasting in birds. *Canadian Journal of Zoology*, 66:159-166.
- Deutsch, C. J., D. E. Crocker, D. P. Costa, and B. J. LeBoeuf. 1994. Sex- and age-related variation in reproductive effort of northern elephant seals. In B. J. LeBoeuf and R. M. Laws (eds.), *Elephant seals: Population ecology, behaviour and physiology*, pp. 169-210. University of California Press,, Berkeley.
- Donohue, M. J., D. P. Costa, E. Goebel, G. A. Antonelis, and J. D. Baker. 2002. Milk intake and energy expenditure of free-ranging northern fur seal, *Callorhinus ursinus*, pups. *Physiological and Biochemical Zoology*, 75:3-18.
- Fedak, M. A., T. Arnborn, and I. L. Boyd. 1996. The relation between size of southern elephant seal mothers, the growth of their pups and the use of maternal energy, fat and protein during lactation. *Physiological Zoology*, 69:887-911.
- Ferguson, N. S., and B. K. Theeruth. 2002. Protein and lipid deposition rates in growing pigs after a period of excess fattening. *South African Journal of Animal Science*, 32:97-105.
- Hindell, M. A., M. M. Bryden, and H. R. Burton. 1994a. Early growth and milk composition in southern elephant seals (*Mirounga leonina*). *Australian Journal of Zoology*, 42:723-732.
- Hindell, M. A., B. J. McConnell, M. A. Fedak, D. J. Slip, H. R. Burton, P. J. H. Reijnders, and C. R. McMahan. 1999. Environmental and physiological determinants of successful foraging by naive southern elephant seal pups during their first trip to sea. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 77:1807-1821.
- Hindell, M. A., D. J. Slip, and H. R. Burton. 1994b. Possible causes of the decline of southern elephant seal populations in the Southern Pacific and Southern Indian Oceans, *Elephant Seals*, pp. 66-84. University of California Press, Los Angeles.
- Houser, D. S., and D. P. Costa. 2001. Protein catabolism in suckling and fasting northern elephant seal pups (*Mirounga angustirostris*). *J Comp Physiol B*, DOI 10.1007/s003600100214.
- Ihaka, R., and R. Gentleman. 1996. R: A language for data analysis and graphics. *Journal of Computational and Graphical Statistics*, 5:299-314.
- Iverson, S. J., W. D. Bowen, D. J. Boness, and O. T. Oftedal. 1993. The Effect of Maternal Size and Milk Energy Output On Pup Growth in Gray Seals (*Halichoerus-Grypus*). *Physiological Zoology*, 66:61-88.
- Kleiber, M. 1975. *The Fire of Life: An Introduction to Animal Energetics*. R.E. Kreiger Publishing Co., Huntington, NY.
- Kretzmann, M. B., D. P. Costa, and B. J. Le Boeuf. 1993. Maternal Energy Investment in Elephant Seal Pups - Evidence For Sexual Equality. *American Naturalist*, 141:466-480.
- Laws, R. M. 1994. History and present status of southern elephant seals populations. In B. J. LeBoeuf and R. M. Laws (eds.), *Elephant Seals*, pp. 49-65. University of California Press, Los Angeles.
- Lydersen, C., and K. M. Kovacs. 1996. Energetics of lactation in harp seals (*Phoca groenlandica*) from the Gulf of St Lawrence, Canada. *Journal of Comparative*

- Physiology B-Biochemical Systemic and Environmental Physiology*, 166:295-304.
- Lydersen, C., K. M. Kovacs, M. O. Hammill, and I. Gjertz. 1996. Energy intake and utilisation by nursing bearded seal (*Erignathus barbatus*) pups from Svalbard, Norway. *Journal of Comparative Physiology B - Biochemical Systemic and Environmental Physiology*, 166:405-411.
- McConnell, B. J., M. A. Fedak, H. R. Burton, G. H. Englehard, and P. Reijnders. 2002. Movements and foraging areas of naive, recently weaned southern elephant seal pups. *Journal of Animal Ecology*, 71:65-78.
- McMahon, C. R., H. Burton, S. McLean, D. Slip, and M. Bester. 2000a. Field immobilisation of southern elephant seals with intravenous tiletamine and zolazepam. *Veterinary Record*, 146:251-254.
- McMahon, C. R., H. R. Burton, and M. N. Bester. 2000b. Weaning mass and the future survival of juvenile southern elephant seals, *Mirounga leonina*, at Macquarie Island. *Antarctic Science*, 12:149-153.
- . 2003. A demographic comparison of two southern elephant seal populations. *Journal of Animal Ecology*, 72:61-74.
- Nagy, K. A., and D. P. Costa. 1980. Water flux in animals: analysis of potential errors in the tritiated water method. *Am. J. Physiol.*, 238:R454-R465.
- Noren, D. P., D. E. Crocker, T. M. Williams, and D. P. Costa. 2003. Energy reserve utilization in northern elephant seal (*Mirounga angustirostris*) pups during the postweaning fast: size does matter. *Journal of Comparative Physiology B*, DOI 10.1007/s00360-003-0353-9.
- Pullen, M. R. 1988. The Physiology of diving in grey seals (*Halichoerus grypus*) and common seals (*Phoca vitulina*). Thesis, Department of Zoology and Comparative Physiology, University of Birmingham.
- Rea, L. D., and D. P. Costa. 1992. Changes in standard metabolism during long-term fasting in northern elephant seal pups (*Mirounga angustirostris*). *Physiological Zoology*, 65:97-111.
- Reilly, J. J. 1989. The water and energy metabolism of grey (*Halichoerus grypus*) and common (*Phoca vitulina*) seals during breeding. PhD Thesis, University of Wales College of Cardiff.
- . 1991. Adaptations to Prolonged Fasting in Free-Living Weaned Gray Seal Pups. *American Journal of Physiology*, 260:R267-R272.
- Reilly, J. J., and M. A. Fedak. 1990. Measurement of the Body-Composition of Living Gray Seals By Hydrogen Isotope-Dilution. *Journal of Applied Physiology*, 69:885-891.
- Schmidt-Nielsen, K. 1997. *Animal Physiology: Adaptation and environment*. 5 ed. Cambridge University Press, Cambridge.
- Scholander, P. F., V. Walters, R. Hock, and L. Irving. 1950. Body insulation of some arctic and tropical mammals and birds. *Biological Bulletin*, 99:225-236.
- Sparling, C. 2003. Causes and consequences of variation in the energy expenditure of grey seals (*Halichoerus grypus*). PhD thesis, University of St Andrews.
- Thorson, P. H., and B. J. LeBoeuf. 1994. Developmental aspects of diving in Northern elephant seal pups. In B. J. LeBoeuf and R. M. Laws (eds.), *Elephant Seals: Population Ecology, Behaviour and Physiology*, pp. 271. University of California Press, Berkeley.
- Trillmich, F. 1996. Parental Investment in Pinnipeds. *Advanced Study of Behaviour*, 25:533-577.

Whittemore, C. T. 1998. *The science and practice of pig production*. 2 ed. Blackwell Science Ltd., London.

**CHAPTER 3: BLUBBER AND BUOYANCY:
MONITORING THE BODY CONDITION OF
FREE-RANGING SEALS USING SIMPLE DIVE
CHARACTERISTICS**

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Abstract

Elephant seals regularly perform dives during which they spend a large proportion of time drifting passively through the water column. The rate of vertical change in depth during these “drift” dives is largely a result of the proportion of lipid tissue in the body, with fatter seals having higher (more positive or less negative) drift rates compared to leaner seals. We examined the temporal changes in drift rates of 24 newly weaned southern elephant seal (*Mirounga leonina*) pups during their first trip to sea to determine if this easily recorded dive characteristic can be used to continuously monitor changes in body composition of seals throughout their foraging trips. All seals demonstrated a similar trend over time: drift rates were initially positive, but decreased steadily over the first 30-40 days after departure (Phase 1), corresponding to seals becoming gradually less buoyant. Over the following ~100 days (Phase 2) drift rates again increased gradually, while during the last ~20-45 days (Phase 3) drift rates either remained constant or decreased slightly. The daily rate of change in drift rate was negatively related to the daily rate of horizontal displacement (daily travel rate), and daily travel rates of more than ~ 80 km were almost exclusively associated with negative changes in drift rate. We developed a mechanistic model based on body compositions and morphometrics measured in the field, published values for the density of seawater and various body components, and values of drag coefficients for objects of different shapes. We used this model to examine the theoretical relationships between drift rate and body composition, and carried out a sensitivity analysis to quantify errors and biases caused by varying model parameter. While variations in seawater density and uncertainties in estimated body surface area and volume are unlikely to result in errors of more than $\pm 2.5\%$ in estimated lipid content, variations in drag coefficient can lead to errors of 10% or

more. Finally, we compared the lipid contents predicted by our model with the lipid contents measured using isotopically labelled water, and found a strong positive correlation. The best fitting model suggests that the drag coefficient of seals while drifting passively is between ~ 0.49 (roughly corresponding to a sphere-shaped object) and 0.69 (a prolate spheroid), and we were able to estimate relative lipid content to within about $\pm 2\%$ lipid. Our results suggest that this simple method can be used to estimate the changes in lipid content of free-ranging seals while at sea, and may help improve our understanding of the foraging strategies of these important marine predators.

Introduction

With the development of time depth recorders (Kooyman, 1965) and satellite, VHF and acoustic telemetry (e.g. Fancy et al., 1988; Fedak, 1992; Fedak et al., 1983; McConnell, 1986) it is now possible to study the behaviour of many of free-ranging marine organisms. Although these data have provided new insights into the foraging ecology of marine species, there are still limitations in the types of information that can be collected. Specifically, direct observation or recording of feeding events is often impossible (particularly for animals ranging over large areas during extended trips), and it is consequently difficult to determine where and when individuals encounter and ingest food, and how much of this is assimilated into the body energy stores. In some cases, instrumented individuals can be recaptured when they return to land, and their net growth, energy expenditure and change in body condition can be estimated and correlated with at-sea behaviour (Bost et al., 1997; Boyd et al., 1993; Boyd and Arnborn, 1991; Chappell et al., 1993; Kooyman et al., 1992; Le Boeuf et al., 2000). However, this only provides information on the relationship between body condition and the behaviour and movements integrated over months and thousands of kilometres, while we are frequently interested in these relationships over scales of weeks and a few kilometers, in order to more accurately correlate animal behaviour to fine-scale environmental features. To determine the timing and spatial pattern of food encounter at these finer scales, one must generally rely on indirect indices, such as movement patterns (e.g. Bell, 1991; McConnell, 1986), dive shape characteristics and/or measures of diving effort (Georges et al., 2000; Guinet et al., 2001; Lesage et al., 1999; Schreer and Testa, 1996). Although these methods have been useful for identifying potentially important foraging habitats, the degree to which these correspond to the rate of prey encounter and ingestion is still uncertain. Moreover,

even if rates of prey encounter and ingestion could be inferred from these indices, they still do not provide information on the energy balance of the individual. For instance, an animal may have a high rate of prey encounter and capture, but may still be in a negative energy balance if its activity and metabolic rates are high. Without information about these links, we cannot correctly estimate the food requirements and energy budgets of animals at sea.

Prey ingestion has been estimated by measuring changes in stomach or oesophageal temperature in seabirds (Garthe et al., 1999; Weimerskirch and Wilson, 1992; Wilson, 1992), sharks (Klimley et al., 2001), penguins (Charrassin et al., 2001; Putz and Bost, 1994; Putz et al., 1998), turtles (Tanaka et al., 1995) and seals (Bekkby and Bjorge, 1998; Gales and Renouf, 1993; Hedd et al., 1996). Although these techniques are useful for recording the timing of feeding events, estimates of meal size have generally been less reliable (Wilson et al., 1995), and the technique is further hampered by short retention times of stomach tags (Wilson et al., 1998). More recently, video and/or image recording instruments have been attached to seals and cetaceans in order to record the timing and rate of prey encounter (Davis et al., 1999; Hooker et al., 2002; Sato et al., 2002a), but the size of the resulting image data sets are often too large to be practical for deployments over more than a few days. Moreover, this technique only reveals what an animal encountered and not what it ingested, and because the body condition of an animal represents a balance between energy assimilation and expenditure, information about the timing of feeding and meal size is not sufficient for estimating the energy balance of an animal.

An alternative strategy is to use aspects of an animals' diving behaviour, as measured by existing data recorders to indirectly estimate changes in body composition. One such approach is to monitor changes in the buoyancy of an animal through changes in measured dive characteristics (Beck et al., 2000; Crocker et al., 1997). In deep-diving phocids such as the elephant seal (*Mirounga* sp.), the buoyancy of an individual is determined primarily by its body composition, and particularly by the ratio of lipid to lean tissue (Crocker et al., 1997; Webb et al., 1998). While lean tissue is denser than seawater, lipid tissue is less dense, and animals with a large proportion of lipid will therefore be more buoyant (Beck et al., 2000; Lovvorn and Jones, 1991a; Lovvorn and Jones, 1991b; Nowacek et al., 2001; Webb et al., 1998). Phocids that have seasonal cycles of terrestrial fasting and at-sea foraging, demonstrate large fluctuations in body composition, and this should be reflected by changes in buoyancy (Beck et al., 2000; Crocker et al., 1997; Webb et al., 1998). Buoyancy may be estimated while an animal is drifting passively through the water column, and this behaviour is regularly observed in dive records from elephant seals (Crocker et al., 1997; Hindell et al., 1998; Le Boeuf et al., 1992). Drift dives were first defined by Crocker et al. (1997), and are broadly characterized by a rapid descent phase during which seals swim actively, followed by a prolonged phase of slower descent or, less commonly, ascent during which seals are assumed to drift passively through the water column. The drift phase is typically followed by a period of active swimming and fairly rapid ascent to the surface. Although the function of drift dives is not clear, Crocker et al. (1997) suggested that they may play a role in food processing, predator avoidance and/or resting. We expect the rate of vertical descent or ascent during the drift phase to vary monotonically with the buoyancy of an animal, and this drift rate may therefore be used to track changes in an animals body condition while at sea.

Although this was demonstrated for female northern elephant seals (*M. angustirostris*) by Crocker et al. (1997), they did not model these relationships to estimate the body condition of seals while foraging at sea using changes in drift rate.

Although the drift rate of a phocid seal will be determined largely by the proportions of lipid and lean tissue, it will also be affected by a variety of external and internal factors. By definition, the constant rate of vertical displacement (i.e. the terminal velocity) of an object moving through a medium occurs when all forces acting upon the object (i.e. gravity, buoyant force and drag resistance) are in equilibrium. The buoyant force is determined by the difference in density between the object and the surrounding medium, while the drag resistance is affected by the surface area and shape of the object, the density of the surrounding medium, and the speed at which the object moves through this medium (Vogel, 1981). In terms of a seal drifting passively through water, the terminal velocity will be influenced by external characteristics such as seawater density that varies with salinity and temperature. It will also be influenced by physiological and behavioural changes such as residual air in the lungs and the orientation of the seals' body in the water. The interactions of all these variables will determine the accuracy with which the body composition of a seal can be estimated from observed drift rate.

In this study we used ARGOS satellite telemetry (Argos, 1989) to relay dive and location data from recently weaned southern elephant seals (*M. leonina*) from Macquarie Island during their first trips to sea. These data were used to describe the change in drift rate of individuals over time. To estimate the accuracy of estimating buoyancy and body composition of individual seals from observed drift rates, we

developed a theoretical mechanistic model of a typical seal pup, and examined the relative contributions of various potential error sources. Finally, we assessed the accuracy of our model by comparing the body composition of a seal predicted from drift rates just after departure from Macquarie with the body composition measured just before departure. Throughout this paper we have adopted the operational definition of body composition as referring to the percent body lipid.

Materials and Methods

Study animals and capture

We selected our study animals from a larger sample of individually marked, recently weaned southern elephant seal pups from the northern isthmus breeding colony at Macquarie Island (54° 30'S, 158°57'E). These pups had previously been weighed and measured at birth and weaning as part of a large-scale mark/recapture program (McMahon et al., 2000b). The study was done in two stages. In the first stage we deployed 44 instruments (32 in 1995 and another 12 in 1996) to study the ontogeny of migration and diving behaviour in naïve pups (Hindell et al., 1999; McConnell et al., 2002). In the second stage we deployed another 23 instruments on female pups (15 in 1999 and 8 in 2000) as part of a detailed investigation of changes in body composition and survival of pups after weaning.

Seals were captured and weighed according to McMahon et al. (2000a). The axial girth was measured immediately caudal to the base of the pectoral flippers, and the length was measured as the straight line between the tip of the nose to the tip of the tail (referred to as standard length, or STL). Seals were then lightly sedated with an intravenous dose of tiletamine/zolazepam (Zoletil® 100 (Virbac, Australia), or

Telazol[®] (Wildlife Pharmaceuticals Inc., USA), at an approximate dose rate of 0.2 - 0.4 mg/kg (Field et al., 2002). Satellite Relayed Data Loggers (SRDLs, Sea Mammal Research Unit, UK) were glued to the fur on the head or upper neck region using two-component industrial epoxy glue (Hilti, Silverwater NSW, Australia), according to the methods described in Fedak et al. (1983), Hindell et al. (1999) and McConnell et al. (2002). We monitored the breeding beaches on a daily basis, and if seals were still present at the colony more than one week after deployment, they were captured again and re-weighed.

Body composition

In 1999 and 2000, we used isotopically labelled water (e.g. Nagy and Costa, 1980; Reilly and Fedak, 1990) to measure the body composition of pups at weaning, prior to departure and upon return to the island. Immediately after sedation, a blood sample was collected from the extradural vein to measure the background isotope level. A weighed dose of approximately 2 μ Ci tritiated water (³HHO) in 4 mL of distilled water was then injected with a 5 mL plastic syringe. The syringe was flushed with blood three times to ensure complete delivery of the ³HHO. A second blood sample was taken 2-3 hours after initial injection for determination of dilution space and calculation of body composition. Blood samples were centrifuged and the plasma transferred to 2 mL cryo-tubes and these were stored at -20°C until further analysis.

We analysed plasma samples for ³H specific activity by liquid scintillation counting. Weighed plasma samples of approximately 100 μ L were added to 10 mL of PicoFlour scintillation cocktail (Packard Instruments) and counted in triplicate for 10 minutes on a Packard Tri-Carb[®] 2000 liquid scintillation counter. Correction for quenching was

made by automatic external standardization. We prepared standard dilutions by gravimetric dilution of an aliquot of the injectate to the approximate dilution expected in the seals, and these were also counted in triplicate for 10 min. The exact water content of each plasma sample was determined by transferring ~100µl of the sample to a weighed glass slide. The slide was weighed again and then dried on a hot plate at a temperature of ~ 50°C until complete evaporation of the plasma water, and the slide was then weighed a third time. In this way we could correct the specific activity of ³H for the exact plasma water content.

We calculated total body water (*TBW*) according to the empirically derived equation for grey seals (*Halichoerus grypus*) (Reilly and Fedak, 1990) as:

$$TBW = -0.234 + 0.971(^3HHO_{space}) \quad \text{Equation 1}$$

The amount of lipid (*TBL*) and protein (*TBP*) expressed as percent of body mass (*BM*), total body ash (*TBA*) and the total body gross energy (*TBGE*, expressed in Megajoules (MJ)) were calculated according to the same authors as:

$$\%TBL = 105.1 - 1.47(\%TBW) \quad \text{Equation 2}$$

$$\%TBP = 0.42(\%TBW) - 4.75 \quad \text{Equation 3}$$

$$TBA = 0.1 - 0.008(BM) + 0.05(TBW) \quad \text{Equation 4}$$

$$TBGE = 40.8(BM) - 48.5(TBW) - 0.4 \quad \text{Equation 5}$$

On-board data interpretation and compression

Satellite Relay Data Loggers (SRDLs) collect and store dive parameters using various sensors, and later relay dive records in compressed form via the ARGOS system.

Depth was measured by the pressure transducer and circuitry on board the SRDL (Keller PA-7, Keller, Winterhur, Switzerland). The output from the depth transducer was sampled with 16 bit A/D such that, after calibration and offset correction, it provided an accuracy of 0.20 m.. Swim speed was recorded by a turbine odometer (Logtron, Flasch Elektronik GmbH, Germany Stall speed $\leq 0.25\text{m/s}$) housed in a polyurethane dome on top of the SRDL housing. Because the SRDL was mounted on the dorsal surface of the head, it would only be expected to respond to movement through the water if the seal was swimming nose first. The SRDLs recorded data every four seconds throughout a dive and at the end of each dive these data were processed and compressed by the on-board microprocessor and stored in the short-term memory before being relayed via the ARGOS satellite system. The details of the compression algorithm are described in Fedak et al. (2001) and the general telemetry system is presented in Fedak et al. (2002). The dive data stored and transmitted back from the instrument make up two categories: 1) Summary dives, for which only maximum dive depth and duration are stored and transmitted and 2) Detailed dives, for which all inflection points and speed data are calculated and transmitted. The transmitted parameters describing a detailed dive are 1) total dive time, 2) the four most important inflection points (d1 to d4, Figure 1) with the most rapid change in dive trajectory, and 3) three average swim speeds (V1 to V3, Figure 1). The first average swim speed (V1) is calculated from all recorded swim speeds between the start of the dive and the first inflection point (d1), V2 is calculated between d1 and d4, and V3 between d4 and the end of the dive (Figure 1).

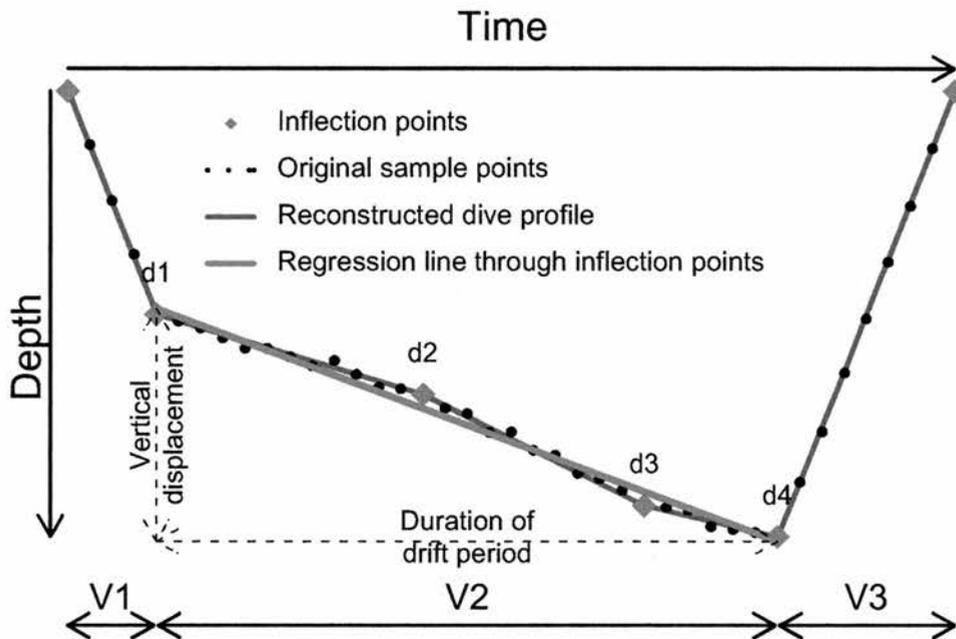


Figure 1. Schematic representation of a drift dive, showing the original sampling points, the inflection points stored and transmitted by the SRDL, and the reconstructed time-depth profile. The drift rate is calculated as the slope coefficient for the best fitting regression line. Here, only the regression line for the entire segment between d_1 to d_4 is shown, but in the actual selection process three different regression lines were evaluated (see text for further details).

Selection of drift dives

We used a combination of methods for selecting drift dives for analysis, and because of differences in the software controlling the SRDLs data collection and compression used in different years, the combination of selection criteria varied between instruments. The first criterion for the selection of drift dives was that V_2 is equal to zero (i.e. $<$ the stall speed), while v_1 and/or $v_3 > 0$. There are two problems with the method described above; 1) the speed sensor can sometimes get blocked by debris, resulting in erroneous recordings of swim speeds of 0, and 2) the putative drift phase of a dive does not always correspond to the total time between d_1 and d_4 for which

V2 is measured (see also the description for the second criterion below), and actual drift dives may therefore occasionally have a $V2 \neq 0$. We therefore used a second criterion based on the dive profile rather than swim speed. The shape of the putative drift segment was examined by fitting different regression lines through; a) all inflection points or excluding b) the first or c) the last inflection point. We used the line of best fit by selecting the model with the lowest mean squared residual (MSR), and the corresponding interval was selected as the putative drift phase. The drift rate (in cm/s) was defined by the slope coefficient for the regression line of the selected segment. The MSR of the best fitting line also provided an “index of linearity” of the selected phase. After initial visual examination of 1000 dive shapes and their corresponding MSR values, we subsequently rejected all dives with a $MSR > 5 \text{ m}^2$.

The final criterion was based on maximum dive depth and the duration of the putative drift phase. We only selected dives where the depth of the shallowest inflection point was at least 10 meters and where the drift phase represented more than 40% of the total duration. Although these criteria may have excluded some shallow drift dives of short duration, the drift phase for these dives would be too short to allow a meaningful estimate of drift rate to be calculated. It also minimized the risk of including dives for which air left in the airways may have a significant effect on the buoyancy of an animal (see detailed discussion below).

Overview of numerical and statistical analyses

Once drift dives had been selected we went through a series of analyses to test their usefulness for predicting body condition. 1) We used a smoothing algorithm to fit a function to the drift rate records for each individual seal, allowing us to define a

representative daily value of drift rate. 2) Daily changes in drift rate were calculated from these fitted values. The predictive functions were then inspected to define phases of the trip with contrasting characteristics, and these definitions were compared to one commonly used criterion for defining putative travelling and foraging phases: daily travel rate. 3) We constructed a mechanistic model of drift dives in relation to body composition, morphometrics (i.e. surface area and volume), residual lung volume, drag coefficient (C_D) and seawater density. We tested the sensitivity of this model to variations in the parameter values for these variables using bootstrap resampling. 4) Finally, we tested the model by comparing the predicted body composition immediately after departure with the body composition measured immediately before departure using labelled water.

Time series and fitted daily values

We used a non-parametric smooth spline technique (`smooth.spline`, Venables and Ripley (1994) as implemented in the R package (Ihaka and Gentleman, 1996)) to fit a predictive function to the time series of drift rates for each individual seal. The fitted values from these curves were taken to represent the expected drift rate for an individual seal on a given day. Spline functions divide the range of observed values by an ordered set of points (knots) along the x (time)-axis. Within each interval the fitted curve is a cubic polynomial, and over the whole range the fit is further constrained to have continuous first and second derivatives at the knot locations. The curve is normally fitted by generalised cross-validation (GCV) (Gu and Wahba, 1991; Venables and Ripley, 1994), resulting in a curve that represents the best compromise between goodness-of-fit and degree of smoothness. We constrained the algorithm further by setting the initial intervals between knots to 14 days. The final interval

length was then fine-tuned by the GCV algorithm. We chose 14 days as our interval to reduce the risk of over-fitting due to occasional high sensitivity to local minima, while also allowing for biologically realistic changes in drift rate expected to be detectable over a period of 5-6 days (see Methods and Results sections).

Prior to fitting the spline curve, we square transformed the drift rate values. This was done because the quadratic relationship between drag and velocity (see Equation 8) results in a time record of change in drift rate with marked discontinuities around zero drift rate (i.e., neutral buoyancy). Transforming the drift rates prior to fitting allowed us to obtain a more continuous distribution, thereby aiding the spline fitting algorithm. The squared drift rate values, along with the fitted daily values, were then back-transformed for further analyses.

Correlation with travel rate

It is common in analyses of animal movements to divide trips into different periods of putative travelling and foraging, and one way to do this is by defining some threshold value for daily horizontal displacement (see e.g. Hindell et al., 1999; McConnell et al., 2002). In order to examine how daily horizontal displacement (hereafter referred to as “travel rate”) corresponds to drift rate, we also defined three phases based on daily changes in observed drift rate. Following Hindell et al. (1999) and McConnell et al. (2002), we determined the transitions between phase 1 and 2 and between phase 2 and 3 respectively as the first and last days where the five-day running average of daily travel rate was less than 20 km. This horizontal displacement is the net displacement over a 24-hour period, and may or may not correspond to the total distance travelled over the same period depending on the directionality of the movements taken by the

animal. In terms of drift rates, we defined these transitions as the first and last days when an individual seal showed a positive daily change in the smoothed drift rate. In order to define the maximum change in drift rate likely to be observed for a given daily travel rate, we performed quantile regressions (Koenker and Bassett, 1978) as implemented by the `rq` function in the R package `quantreg`. This function fits conditional regressions through a specified quantile (in this case the 90th quantile) of a response variable.

Drift rate and body composition

To test the accuracy of body composition estimated from drift rates, we developed a theoretical mechanistic model of drift rate for a hypothetical average elephant seal pup at Macquarie Island. Typical values for standard nose-to-tail length (*STL*), and axial girth (*AG*) were taken from all pups captured as part of the larger study in 1998, 99 and 2000, investigating body composition of pups. For simplicity, we kept the volume of the pup constant at 100 l, and varied the lipid content between 10 and 60 %. The proportions of other body components were then derived from equations 2–5 above. The total density of the seal over the range of body compositions, according to:

$$\rho_{seal} = (\rho_l \times P_l) + (\rho_p \times P_p) + (\rho_b \times P_b) + (\rho_{bw} \times P_{bw}) \quad \text{Equation 6}$$

where ρ = density of component, P = proportion of component subscripts l , p , b and bw indicate lipid, protein, bone mineral (ash) and body water respectively (e.g. $P_l = 0.01 \times \% TBL$ from Equation 2 above). We used published values for the density of various body components in humans (Moore et al., 1963). These values were: $\rho_l =$

0.9007 g/cm³, $\rho_p = 1.340$ g/cm³, $\rho_b = 2.300$ g/cm³, and $\rho_{bw} = 0.994$ g/cm³. We then modelled the buoyant force according to (Vogel, 1981) as the difference between the total density of the body and the surrounding seawater as:

$$BF = (\rho_{sw} - \rho_{seal}) \times V \times g \quad \text{Equation 7}$$

where BF is the buoyant force in Newtons, ρ_{seal} is the density of the seal in g/cm³, ρ_{sw} is the density of the surrounding seawater, V is the volume of the seal in cm³, and g is the gravity constant. The drag force of the seal was estimated by:

$$D = \frac{1}{2} \times C_D \rho_{sw} S U^2 \quad \text{Equation 8}$$

where C_D is the dimensionless drag coefficient, S is the surface area of the seal in m², and U is the terminal velocity in m/s (Vogel, 1981). The theoretical drift rate could then be calculated as the terminal velocity by equating the previous two equations:

$$U = \sqrt{2 \times \frac{(\rho_{sw} - \rho_{seal}) V g}{C_D \rho_{sw} S}} \quad \text{Equation 9}$$

Using this equation, we could then quantify the relative importance of variations in seawater salinity & temperature, seal surface area and C_D on the predicted drift rate. The maximum and minimum seawater densities were calculated based on the maximum salinity, temperature and depth ranges likely to be encountered by elephant seals from Macquarie Island. The temperature and salinity ranges were taken from (Gordon, 1988), and were 0 - 6° C and 33.9 – 34.7 ‰ respectively. The depth range

over which seawater densities were calculated was set to 0 – 500 m. The surface area of the seal was initially modelled as two opposing cones with a common base, the circumference of which corresponded to the axial girth of a typical seal pup (135 cm). The anterior cone was assumed to have a height corresponding to 1/3 of the average standard STL of a typical seal pup (135 cm), while the posterior cone had a height of 2/3 of the average STL. Williams and Kooyman (1985) reported a C_D of 0.09 for a harbour seal (*Phoca vitulina*). However, this was for an actively swimming animal, travelling headfirst and thereby minimising drag. It is unlikely that a passively drifting seal will move in the same streamlined orientation, and we therefore tested a range of coefficients. Here, we assumed a Reynolds number of a seal in $\sim 10^\circ\text{C}$ water of $\sim 60,000$ at a speed of 0.25 m/s, and $\sim 120,000$ at a speed of 0.5 m/s. This gives C_{Ds} of ~ 0.47 for a sphere and 1.17 for a cylinder travelling crosswise. In our initial analyses, we therefore used these three values (0.09 for the harbour seal, 0.47 for a sphere and 1.17 for a cylinder). These values were slightly modified in subsequent analyses (see below).

The total buoyancy of an air breathing aquatic animal is not constant, but will change with depth due to residual air in the lungs, that is compressed at greater depths. We used published equations for the relationship between body size and residual lung volume to test estimate the likely bias caused by this residual air. Kooyman (1989) estimated the residual lung volume of a marine mammal at the onset of a dive to about 50 % of their total lung capacity (TLC), where TLC (in litres) is estimated as:

$$TLC = 0.10(BM)^{0.96}$$

Equation 10

While this equation assumes that TLC is approximately proportional to the total body mass, we instead assumed TLC to be proportional to the lean body mass of the seal. However, while equation 10 estimates the lungs to roughly 10% of total body mass (i.e. a constant of 0.10), we compensated for the use of lean mass instead of total mass for our calculations, and assumed that the lungs represent ~ 12.5% of total lean mass (i.e. a using constant of 0.125). This correction was based on the assumption that the average lean mass of the seals studied by Kooyman (1989) was ~70% of total body mass, and that a lung volume of ~10% of total body mass is roughly equivalent to a lung volume of ~12.5% of lean mass. To simplify our calculations, we also substituted lean mass with lean *volume*, since our model seal had a total body volume set to 100 l. This gave us the following relationship between seal lean volume (V_l), depth (d) and air volume at a given depth (V_{ad}):

$$V_{ad} = \frac{0.0625 \times V_l^{0.96}}{1 + (d / 10)} \quad \text{Equation 11}$$

The estimated density for a seal with a given body composition at a given depth could then be calculated as:

$$\rho_{seal_{ad}} = \frac{\rho_{seal} \times V_l}{V_l + V_{ad}} \quad \text{Equation 12}$$

and this adjusted density could then be used in Equation 9 to calculate the estimated drift rate for the specific depth According to:

$$U = \sqrt{2 \times \frac{\left(\rho_{sw} - \frac{\rho_{seal} \times V_t}{V_t + V_{a_d}} \right) V g}{C_D \rho_{sw} S}}$$

Equation 13

Because seals change depth during drift dives, the residual lung volume will also change, as would the total body density. To simplify our model, we have defined depth as the midpoint between the start and end depth of the drift phase, and thus the predicted drift rate would correspond to the rate halfway through the drift phase.

Model evaluation

1. Simulation test

We tested the sensitivity of the model to the various parameters using a randomised bootstrap procedure. One hundred drift dives were randomly selected from the total sample of observed dives. These dives were selected with replacement (i.e. a dive could be selected more than once), and the drift rate and the depth halfway between the start and end depths of the drift segment (mid-depth) for each of these dives were extracted. For each dive, values of the axial girth (*AG*), standard nose-to-tail length (*STL*), C_D and seawater density were drawn at random from populations of 1000 values, following realistic distributions for these variables; *AG* and *STL* were drawn from normal distributions with means and standard deviations of 1.3 ± 0.1 and 1.5 ± 0.1 m respectively (based on all measurements on pups in the larger body composition study before and after the first trip). Drag coefficients were drawn from a uniform distribution with minimum and maximum values of 0.47 (sphere) and 1.17 (cylinder), and seawater densities were drawn from a uniform distribution with minimum and maximum values of 1.027 and 1.030 g/cm³ respectively. The body surface area and

volume were calculated from the *AG* and *STL* values as previously described, and the volume of residual air in the lungs was calculated based on this body volume for the specific mid-depth value for each of the 100 selected dives.

We then calculated the predicted body density by re-arranging Equation 13, and the predicted lipid content was then derived from this density using equation 6.

$$\rho_{seal} = \frac{\left(\rho_{sw} - \frac{U^2(C_D \rho_{sw} S)}{2V_t g} \right) (V_t + V_{ad})}{V_t} \quad \text{Equation 14}$$

We compared this set of 100 “predicted” lipid contents to a set of “actual” lipid contents that were calculated assuming *STL* and *AG* of 1.5 and 1.3 m respectively, a seawater density of 1.028 g/cm³ and a *C_D* of 0.82, i.e. the average of the *C_D*s for a sphere (0.47) and a cylinder (1.17). We calculated the kernel density distribution of all 100 residuals (predicted – actual lipid contents), and defined the range of errors corresponding to a probability density of >0.025 to obtain 95% confidence intervals for our prediction accuracies. We repeated the whole procedure 1000 times, and thus obtained mean and variance estimates for the confidence intervals of the prediction errors. We first ran this procedure allowing values for all parameters to be randomly selected, and then repeated the procedure keeping all but one of the parameters fixed. This allowed us to estimate how uncertainty in each parameter estimate contributed to the overall error. We also ran two separate series of analyses, one using uncorrected body density values and the other using values corrected for the assumed volume of residual air at the mid-depth of the drift segment. This allowed us to estimate both the likely bias due to residual air in a real data set, and also to determine if the error range

was similar for uncorrected and corrected values. In the first case, uncorrected predicted values obtained from the simulation procedure were compared to uncorrected “actual” values obtained by keeping all parameters fixed (as described above), while in the second case both the predicted and actual values were first corrected for the residual air volume at the mid-depth.

2. Correlation between predicted and measured lipid content

The final test of our model was to compare the lipid contents predicted from drift rates (hereafter referred to as “predicted” lipid contents) with lipid contents measured using labelled water immediately prior to departure (hereafter referred to as “measured” lipid contents), as described above. Because many SRDL records ended well before animals returned to land, we did not include comparisons of predicted and measured lipid contents when seals returned after an extended foraging trip.

In this analysis, the volume (V) and surface area (S) of each individual was calculated from the AG and STL measurements made just prior to departure, assuming the seal was shaped like a prolate spheroid. The functions for calculating volume and surface area were thus:

$$V = \frac{4}{3}\pi r_{AG}^2 r_{STL} \quad \text{Equation 15}$$

and

$$S = 2\pi r_{AG}^2 + 2\pi \frac{r_{AG} r_{STL}}{e} \sin^{-1} e \quad \text{Equation 16}$$

where r_{AG} is the axial radius calculated from the axial girth, r_{STL} is the longitudinal radius calculated as $0.5 \times STL$, and e is calculated as:

$$e = \sqrt{1 - \frac{r_{AG}^2}{r_{STL}^2}} \quad \text{Equation 17}$$

For each dive, we then calculated the residual lung volume as a function of seal volume as described above, using the depth halfway between the start and end depth of the drift segment. Finally, we were then able to determine a predicted lipid content for each dive corresponding to the drift rate of that dive. This gave us individual time series of predicted lipid contents for each individual over the duration of the SRDL record, and representative daily values were again calculated by fitting spline functions (knot intervals = 14 days) to these time series according to the methods described above. The predicted lipid content for each seal at the day of departure was then compared to the lipid content measured for that seal using labelled water. Since the labelled water method gives values for lipid content in mass percent, all lipid contents predicted from drift rates were multiplied by the previously published value of 0.9007 for lipid density (Moore et al., 1963) to convert them from percent by volume to percent by mass.

In this analysis we included C_D as a parameter to be estimated by the model, and tested the fit across the entire range of C_D values, from the harbour seal (0.09) to the cylinder (1.17). We used two different methods for assessing the fit. The first method selected the C_D that gave the smallest sum of squared residuals between predicted and

measured lipid contents. The second method was based on the slope of the regression line between predicted and measured lipid contents, and selected a C_D that gave a slope coefficient of 1. The rationale of using these two methods was that the C_D value giving the smallest absolute errors between predicted and measured lipid contents may have a slope that is significantly different from 1, i.e. that the errors are dependent on the absolute values of lipid content. For instance, a slope >1 would suggest that for fatter animals, the model produces values of lipid content that are underestimated compared to measured lipid contents, while it gives overestimated lipid contents for leaner seals, and vice versa if the slope coefficient is <1 .

Temporal resolution of fitted time series

Our model also allowed us to obtain a rough estimate of the period over which we can detect a true trend in drift rate given the amount of random noise in the data. The daily lipid gain is likely to be relatively small in proportion to the lipid already present in the body. This will affect the time scale over which we can detect a significant change in drift rate. We also expect some variations in drift rate observed within a given day, due to changes in body orientation within and between dives and variations in residual lung volume. To estimate the likely effects of these variations, and to determine the likely temporal resolution of our method, we compared the estimated daily change in drift rate for a feeding seal with the average daily residuals of drift rate (i.e. the difference between each observed drift rate for a given day and the mean drift rate for that day obtained from the fitted spline function). We modified our mechanistic model to estimate the average observed change in drift rate over the foraging period, and to estimate the likely daily change. We again assumed a total body volume of 100 L at departure, of which 38 % is lipid, and 150 L at return 175 days later, of which 32% is

lipid (SMRU, unpublished data). We estimated an average foraging period of 100 days, starting 30 days after departure. We also estimated the volume and body composition at the start of feeding based on the values at departure, assuming that the metabolic rate of a seal while in transit is similar to that on land. Similarly, we estimated the volume and body composition at the end of feeding by back-calculating from values at return to the island 45 days later, again assuming a metabolic rate while in transit similar to that on land. From these values we estimated an average daily change in lipid content and calculated the expected average daily change in drift rate. We could then compare this daily change to the daily residuals. These calculations were done for each seal separately, and the probability distributions of the residuals were modelled as kernel density functions. We selected the residual value corresponding to the maximum kernel density value as our best estimate of within-day variation in drift rate for a given seal. By dividing this value by the estimated average daily change in drift rate we could then determine the minimum time interval over which any changes in drift rate would likely represent a real change in body composition.

All descriptive statistics are presented as mean \pm one standard deviation, unless stated otherwise.

Results

Drift dive extraction and summary

We obtained drift dive records from 24 individual seals that were of sufficient duration and continuity to allow for proper statistical analysis (Table 1). Of these seals, four belonged to the 1996 cohort (three males and one female), 12 from the

1999 cohort (all females) and eight were from the 2000 cohort (all females). In total, 74999 dives with complete profiles were recorded. Of those, 2746 dives fitted our selection criteria for drift dives, and the number of dives extracted for each seal varied from 26 to 210. The average number of drift dives obtained per day for an individual seal varied from 1.23 to 3.74 (2.29 ± 0.58), and the maximum number of dives obtained ranged from 3 to 14 dives per seal daily. Most of the dives extracted (2144 dives) showed a negative slope during the drift segment (hereafter referred to as “negative dives”), while 602 dives showed a positive slope (“positive dives”). The average maximum dive depth of drift dives across all seals (i.e. the deepest depth attained during a given dive) was 133.0 ± 76.3 and 115.0 ± 80.3 m for negative and positive dives respectively, and the maximum depth recorded for each individual varied from 85.2 to 610.4 m. The drift segment generally occurred at depths between about 65 and 117 m (Figure 2) regardless of the direction of the drift. Negative drift segments started at 66.5 ± 59.4 m and ended at 123.0 ± 74.9 m (Figure 2a), while positive segments started at 112.3 ± 79.1 m and ended at 64.2 ± 65.8 m (Figure 2b).

PTT Reference	Year	Dates		Mass (kg)		Duration Record Trip	Positive daily change			Phase duration (days)			Days of		
		Weanin	Departure	Return	Weaning		Departure	Return	First	Max	Last	1	2	3	-
22483_96	1996	19-Oct	05-Dec		92		55	32	38	(48*)	31	(16*)		(14*)	(12*)
26623_96	1996	19-Oct	17-Dec		169		146	47	54	(128*)	46	(81*)		(35*)	(8*)
26624_96	1996	20-Oct	10-Dec		92		136	40	127	(136*)	39	(96*)		(31*)	(34*)
28482_96	1996	21-Oct	20-Dec		171		42	33	42	(42*)	32	(9*)		(8*)	(0*)
28504_99	1999	18-Oct	29-Dec	23-Jun	195	123	175	41	98	159	40	118	18	19	21
2846_99	1999	21-Oct	20-Dec	30-Jun	161	108	183	79	183	183	78	104	10	4	15
22488_99	1999	22-Oct	08-Dec	10-Jun	94	68	182	48	90	130	47	82	55	14	42
28497_99	1999	24-Oct	09-Dec	22-Apr	101	71	115	39	69	115	38	76	20	7	33
26627_99	1999	25-Oct	13-Dec	10-Jun	90	62	176	41	117	169	40	128	11	19	33
2849_99	1999	26-Oct	28-Dec	07-Jul	164	103	144	8	78	144	7	136	48	13	19
28494_99	1999	26-Oct	23-Dec	17-Jun	145	93	94				(94*)			(14*)	(1*)
28496_99	1999	26-Oct	24-Dec		169	108	93	31	56	(66*)	30	(35*)		(46*)	(18*)
20918_99	1999	27-Oct	09-Dec	11-	85	58	119	28	35	119	27	91	35	9	13
17217_99	1999	28-Oct	31-Dec	26-Jun	162	101	144	44	104	144	43	100	34	21	29
26629_99	1999	03-Nov	22-Dec		108	80	107	43	76	(107*)	42	(64*)		(29*)	(41*)
5812_99	1999	12-Nov	23-Dec	10-Jun	93	70	167	39	94	133	38	94	37	27	33
Cleo_00	2000	20-Oct	31-Dec		197	131	225	30	147	198	29	168		28	58
FirstOne_00	2000	26-Oct	25-Nov	30-Apr	78	59	57	7	16	44	6	37	112	16	28
Alice_00	2000	30-Oct	29-Dec	22-Jul	161	106	204	50	78	172	49	122	33	30	25
Ella_00	2000	01-Nov	31-Dec		175	114	98	44	93	(98*)	43	(54*)		(29*)	(38*)
Flora_00	2000	01-Nov	01-Jan		173	119	176	45	154	163	44	118		23	15
Billie_00	2000	06-Nov	28-Dec	17-Jul	180	113	198	58	111	176	57	118	25	54	34
Doris_00	2000	09-Nov	30-Dec	11-Aug	144	95	220	37	165	178	36	141	46	35	45
20918_00	2000	13-Nov	27-Dec	23-	99	68	140	34	41	140	33	106	7	19	29
Mean		27-Oct	20-Dec	15-Jun	137.4	92.5	141.5	39	89.8	147.9	38	108.7	35.1	23	26
Min		18-Oct	25-Nov	22-Apr	78	58	42	7	16	44	6	37	7	4	0
Max		13-Nov	01-Jan	11-Aug	197	131	225	79	183	198	78	168	112	54	58
S.D.		7.6	10.2	30.9	40.2	23.4	51.6	14.6	44.6	36.7	14.6	30.2	26.6	12.31	14.26

Table 1. (Previous page) Details of the 24 Macquarie Island southern elephant seal pups for which drift dives were regularly observed in SRDL records. The departure mass is given as the last recorded mass, typically measured 4.2 ± 3.3 days (Mean \pm SD) prior to the last sighting of the individual at the Isthmus study colony. The departure mass on the actual day of departure was estimated by extrapolation from the last recorded mass at a mean individual daily mass loss rate (the difference between weaning mass and last recorded mass divided by the number of days between them). Since the difference between the last recorded and estimated mass was typically very small (1.8 ± 0.4 kg, or 1.97 ± 0.3 %) we have consistently used the last recorded mass. The record duration is the last day after departure at which data were received from a tag, while the trip duration is the number of days between departure and the first sighting of a seal back at Macquarie Island. The first and last days for which a positive change in drift rate was observed are presented as "First" and "Last", while "Max" presents the day after departure at which the maximum positive change was observed. The phase duration is here given as the number of days between the first and last days for which a positive change in drift rate was observed, and the "Days of change" indicate the total number of days for which a negative ("-") and positive ("+") change in drift rate was observed. An asterisk indicates that the number may not be accurate, because of premature interruption of the record due to tag failure or death of the animal. These numbers were excluded from the calculations of the summary statistics presented at the bottom of the table.

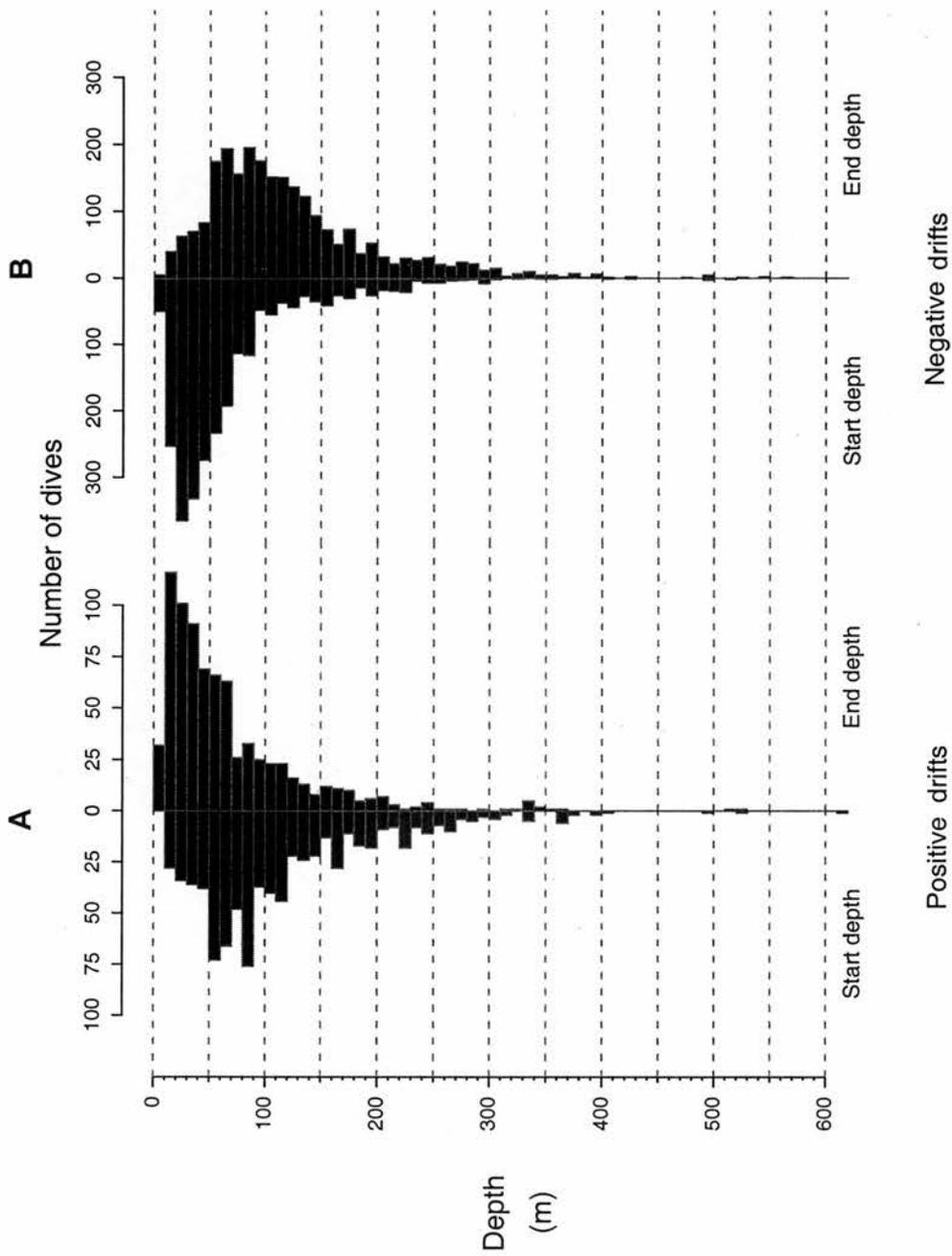


Figure 2. Histograms showing the frequency distribution (in 10 m intervals) of start (red) and end (black) depths for the drift segments of negative and positive drift dives separately.

The frequency distribution of drift rates showed a clear bimodal pattern, and very few dives had a drift rate around zero (see left-hand histogram in Figure 6). Negative drift rates were on average -19.9 ± 8.2 cm/s while positive rates were 16.0 ± 11.9 cm/s. The 95% probability density range of observed drift rates was -33.4 to 23.1 cm/s.

Time series, fitted values and resolution

Time series with fitted spline curves are presented in Figure 3. Although there were distinct individual variations, a clear general pattern of change in drift rate over time could also be seen. Trips could be broadly defined by three distinct phases similar to those obtained using daily travel rates (see e.g. Hindell et al., 1999; Le Boeuf et al., 2000; McConnell et al., 2002 and results and discussion below). The first phase lasted about 30–50 days, and most seals showed a gradual decrease in drift rate. Some seals initially had positive drift rates (i.e. they drifted upwards during the passive phase), but they all showed exclusively negative drift rates (i.e. sinking) by the end of this first phase. The second phase was characterised by an initial levelling out followed by a gradual increase in drift rate. Except for cases where the record stopped prematurely due to tag failure, loss or death of the animal, this second phase lasted roughly 100 days. Most of the seals showed positive drift rates at the end of this phase. In cases where the record lasted longer than the duration of phase 1 and 2, the drift rate either remained constant or decreased slightly throughout the third phase, until the end of the record.

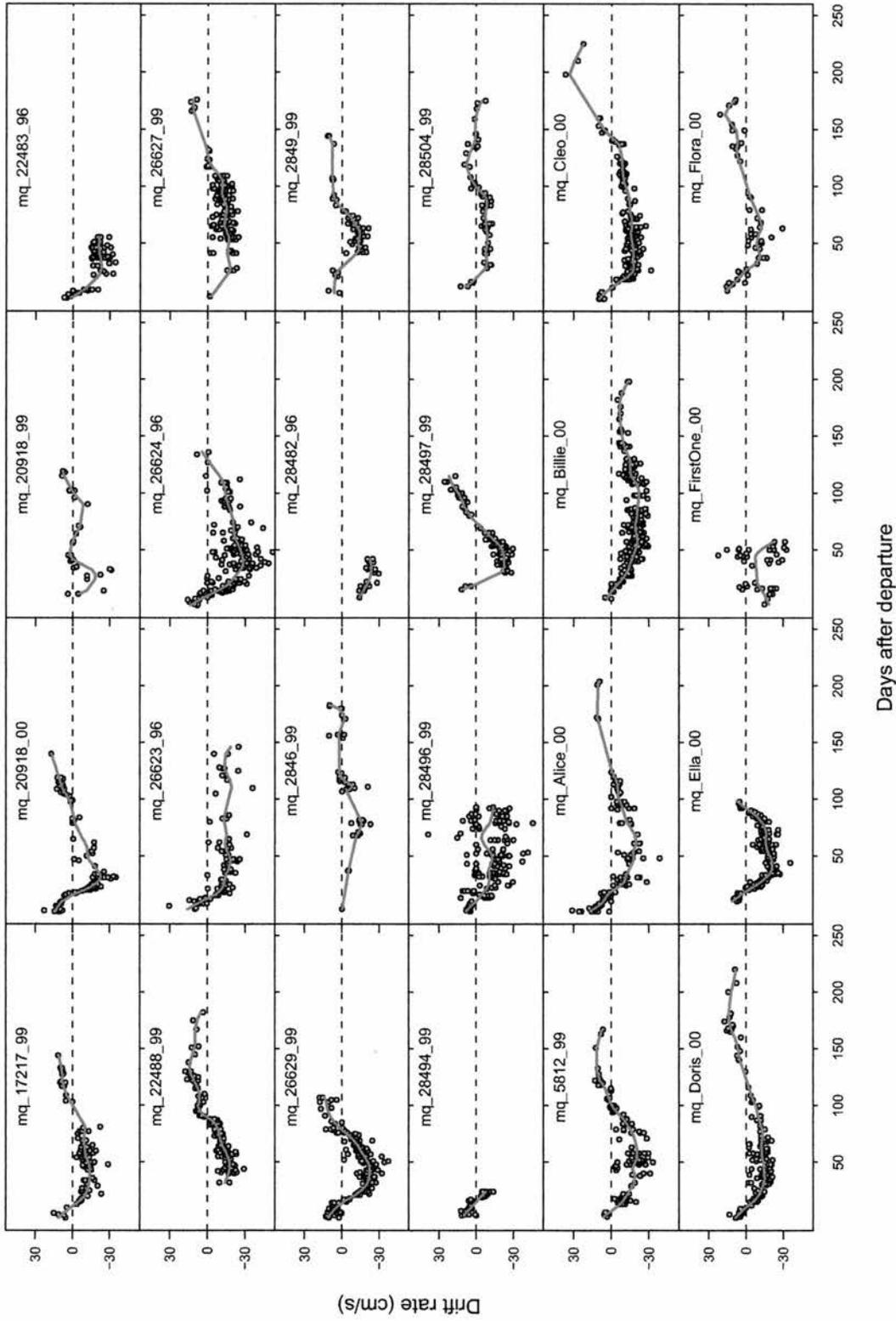


Figure 3. Time traces of drift rates for each individual seal over the course of the first trip to sea. Each point represents a drift dive, while the solid lines represent smoothed spline functions fitted by the GCV algorithm, constrained to an initial interval between spline knots of 14 days (see text).

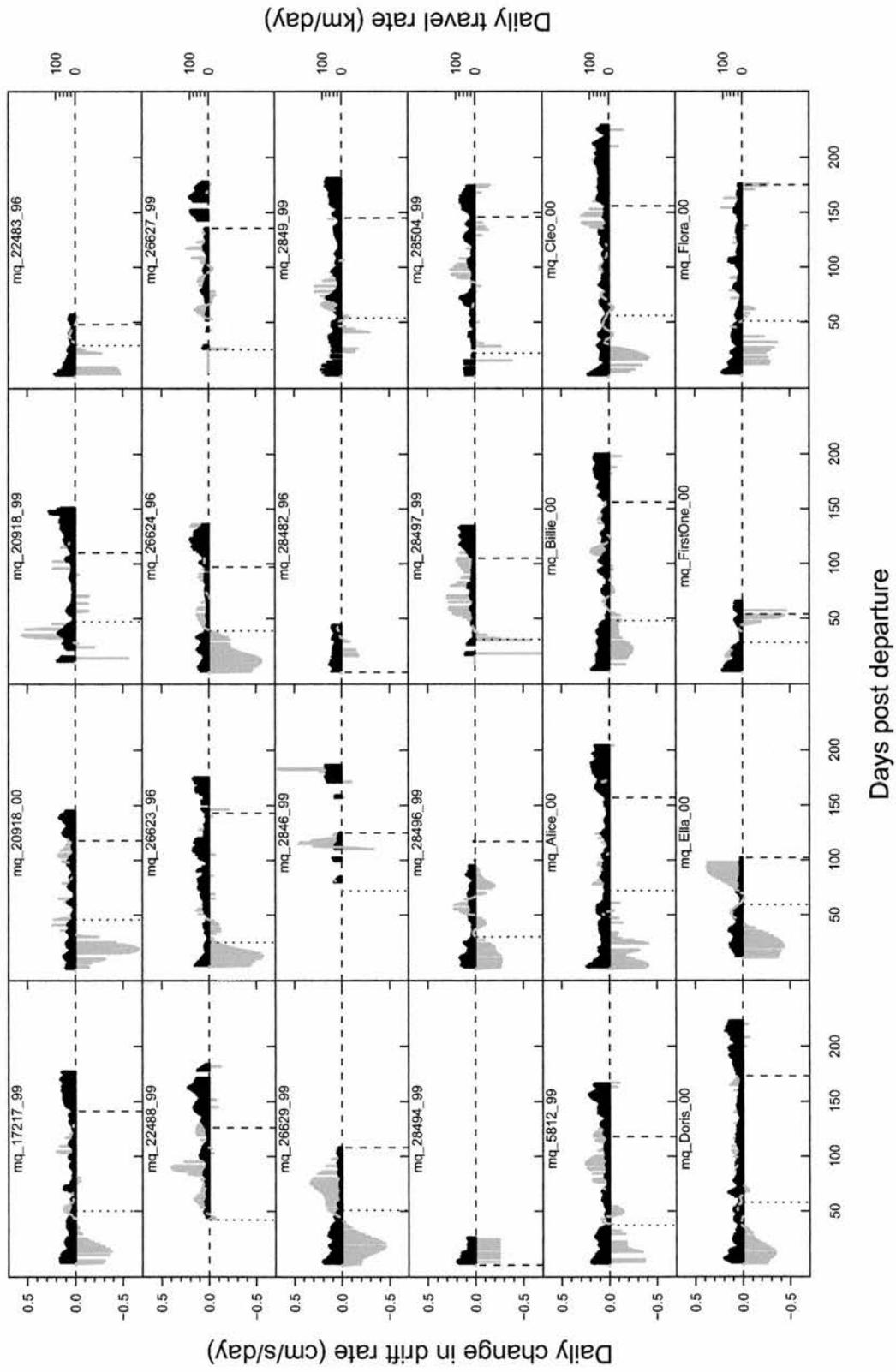


Figure 4. Daily change in drift rate (grey bars) and daily travel rate (daily horizontal displacement, black bars) for individual seals over the course of the first trip. The vertical solid and dashed lines indicate the switch between phase 1 and 2 respectively, based on the first and last day with a five-day running average of daily travel rate below 20 km (McConnell et al., 2002).

There were large individual variations in drift rate changes over the course of the trip (Figure 4). While some seals (e.g. 26629_99 and 28497_99) appeared to have a continuous period of negative change followed by a continuous period of positive change, others (most notably Billie_00 and Cleo_00) switched repeatedly between positive and negative change. The transitions between phases based on daily change in drift rate corresponded reasonably well with previous criteria using daily travel rate. For instance the switch from negative to positive change in drift rate after the initial “transit” period was generally associated with a sudden decrease in travel rate (Figure 4). In general, the 90th quantile regressions of daily change in drift rate against daily travel rate indicated an upper “edge” in the change in drift rate for any given daily travel rate. Although there were large individual variations, seals generally showed positive changes in drift rate only during days when their travel rate was less than ~50 – 90 km/day (median = 75.1 km/day; sd = 31.3 km/day), while negative changes in drift rate occurred at all travel rates (Figure 5).

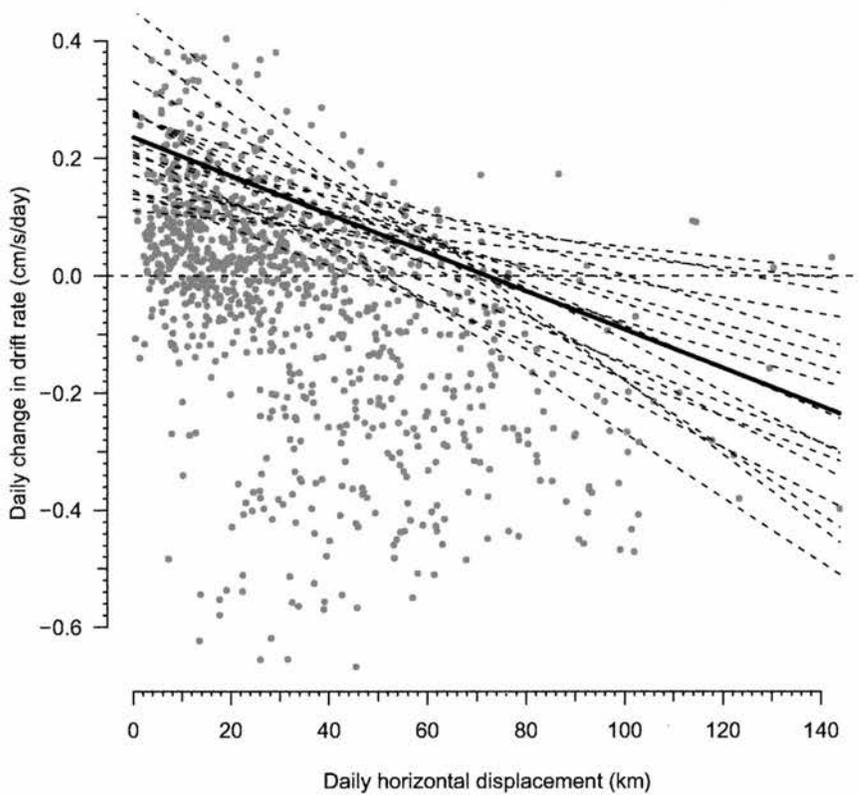


Figure 5. Daily change in drift rate plotted against daily horizontal displacement (i.e. the distance between average daily locations). Each red point represents a drift dive. The thin dashed lines represent the 90th quantile regressions fitted for each individual seal, while the thick solid line represents the line obtained using the average of the slopes and intercepts from each individual 90th quantile regression.

Temporal resolution of time series

The range of residuals of all drift rates for a given day over the fitted value for that day from the spline function varied between individuals from about -0.59 to 0.39 cm/s. The theoretical estimate of the total change in drift rate over the course of the assumed 100-day feeding period was 20 cm/s, corresponding to a daily change of 0.2 cm/s. The residuals corresponding to the maximum kernel probability density was 1.31 ± 0.43 cm/s (all seals combined). When we divided the residual values for each

individual seal by the estimated average daily change (e.g. $1.31/0.2$), we obtained time intervals of 6.45 ± 2.10 days (median = 6 days) over which any changes in drift rate are likely to reflect a biological trend as opposed to random variation.

Theoretical model of drift rate and body composition

Our mechanistic model of the predicted drift rates of an average sized seal across the range of lipid contents is illustrated in Figure 6. The three curves illustrate the variation in the relationship between lipid content and drift rates using various C_D s, while the vertical histogram represents the frequency distribution of all observed drift rates. The relationship between body composition and predicted drift rate shows a clear sigmoid relationship with a high rate of change in drift rate for seals close to neutral buoyancy. This shape is a result of the quadratic relationship between velocity and drag (see Equation 8). Using the C_D of a cylinder (1.17), the predicted drift rates ranged from -34.2 cm/s for a seal with 10 % lipid to 27.5 cm/s for a seal with 60% lipid. The corresponding values using the C_D of a sphere (0.47) are -52.9 and 42.5 cm/s respectively, while the C_D of a harbour seal swimming headfirst (0.09) results in extreme values of -123.5 and 99.2 cm/s respectively.

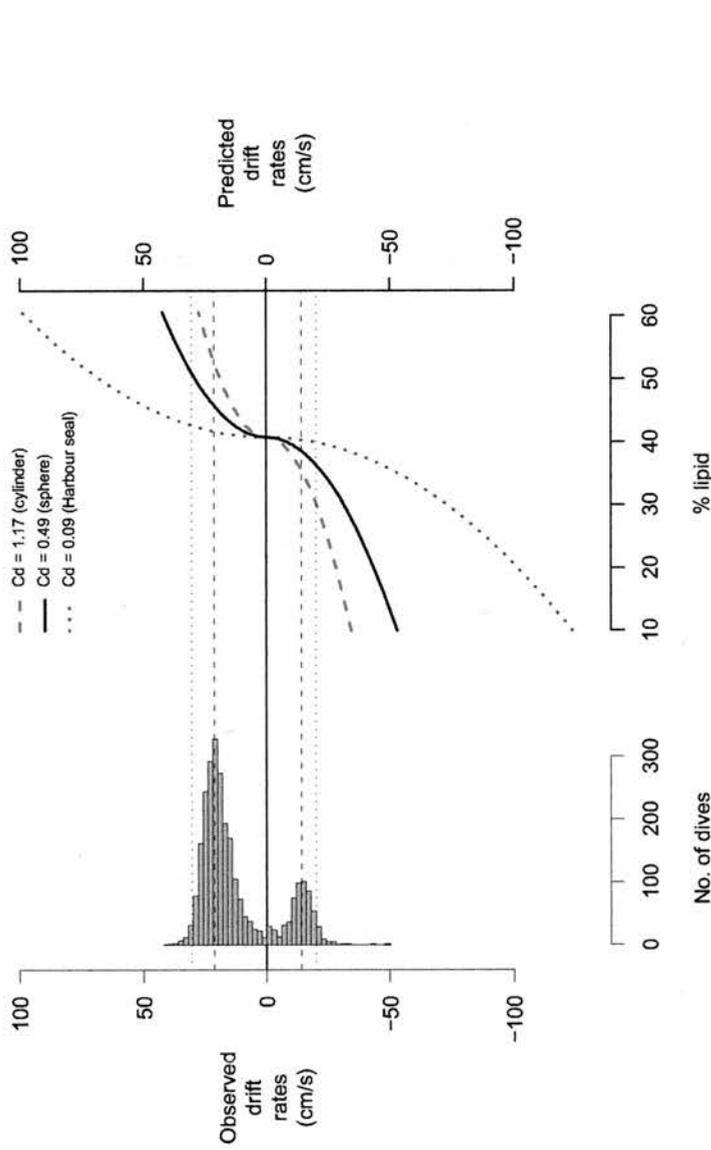


Figure 6. Vertical frequency distribution of observed drift rates (left), and curves representing the predicted drift rates (assuming no residual air) of a seal with a total body volume of 100 l (right). As shown in the legend, the three curves correspond to the predicted drift rates using published C_{DS} for a cylinder (red dotted line) and a sphere (solid black line) from Vogel (1981) as well as for a harbour seal (blue dotted line) from Williams and Kooyman (1985). The horizontal dashed lines represent the maximum kernel density for all observed positive and negative drift rates separately, while the dotted lines represent the range of the 95% probability of occurrence (kernel density function, bandwidth = 2 cm/s).

1. Bias due to residual air in the lungs

Our model suggests that the buoyant force caused by residual air in the lungs can result in a significant positive bias in drift rate (Figure 7a). At shallow dive depths, this extra buoyant force can be of similar magnitude as that caused by body lipid. For instance, at a depth of 10 m, the positive buoyant force attributed to lipid ranges from ~ 22 to 120 N over the range of lipid contents while the corresponding values for residual air is ~ 28 – 14 N over the same range. This means that at 10 m, residual air can provide more than half the total positive buoyant force for a lean seal (~64 % at 10 % lipid), while for a fat seal (60 % lipid) residual air provides just over 10% of the buoyant force. This bias is substantially reduced at greater depths, because of the exponential decrease in volume with increasing depth. For instance, at 50 m, residual air provides ~ 32 % of the buoyant force compared to lipid for a seal with 10 % lipid, while for a seal with 60 % lipid air provides less than 4 % of the buoyant force. At 100 m these figures are further reduced (~ 20 % at 10 % lipid and ~2 % at 60 % lipid). Figure 7b shows the relationship between lipid content and the expected drift rate for the model seal at the same depths as in Figure 7a.

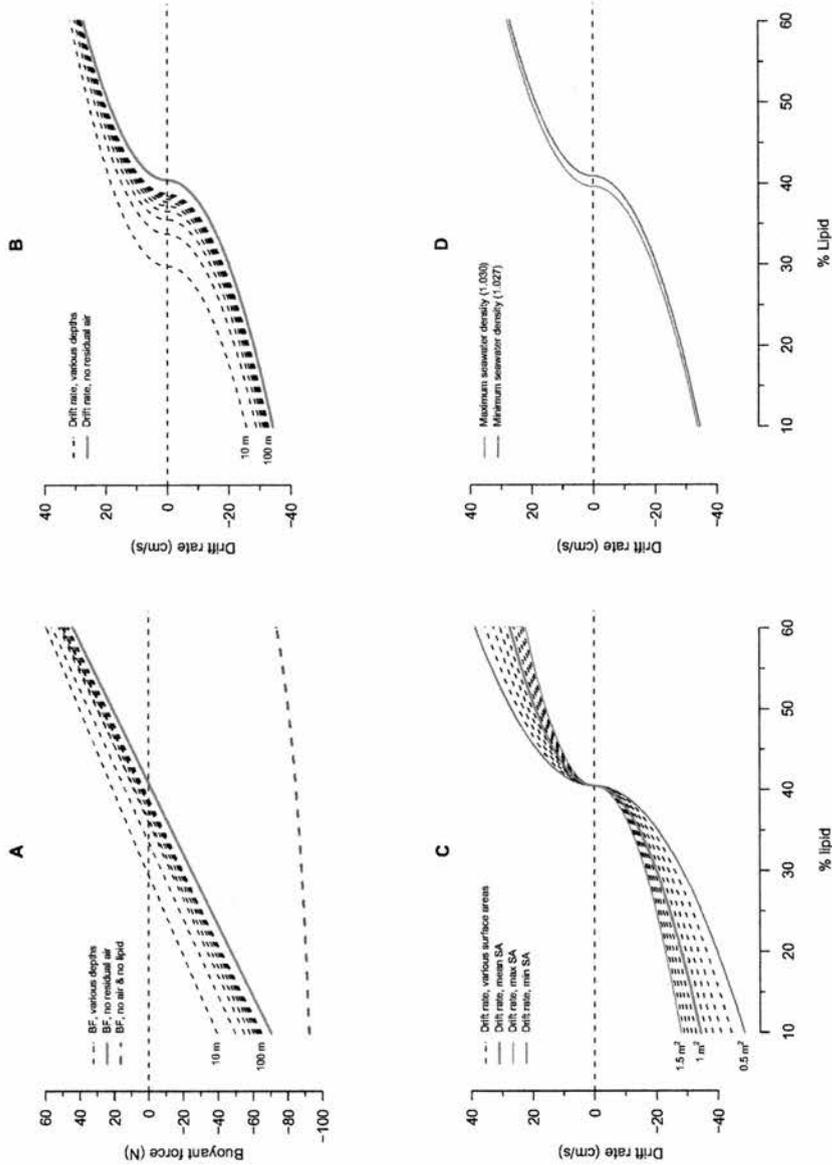


Figure 7. Relationships based on theoretical calculations for a seal pup with a total volume of 100 L. A) Buoyant force attributed to different body components. The thick dashed blue line represents the buoyant force (negative) of the total non-lipid body, while the thick solid red line represents the buoyant force of the whole body including lipid but assuming no residual air. The thin dashed lines represent the buoyant force of the total body, including residual air left in the lungs at 10 m depth intervals from 10 to 50 m. B) Drift rates predicted from Equation 9 for the 100 L seal, assuming a total surface area of 1 m^2 . The thick red line represents the drift rate assuming no residual air in the lungs, while the thin dashed lines represent drift rate accounting for residual air at 10 m intervals from 10 to 100 m. C) Drift rate calculated from Equation 9, assuming no residual air in the lungs. The thick red line represents drift rate assuming a surface area of 1 m^2 (i.e. identical to the thick solid line in Fig 7B), while the thin dashed lines represent the drift rate resulting from variations in surface area. The two extreme values of surface area, 0.5 and 1.5 m^2 , are indicated by the blue and green lines respectively. D) Drift rates calculated from Equation 9 using the minimum and maximum seawater densities (1.027 and 1.030 g/cm^3 , blue and green curve respectively) likely to be encountered by southern elephant seal pups from Macquarie Island. See text for further details.

2. Error due to variations in body surface area and volume

Figure 7c illustrates the relationship between lipid content and theoretical drift rate, allowing for variations in body surface area from 0.5 to 1.5 m². These errors are more pronounced towards the extremes of lipid contents and drift rates, while they approach zero for seals near neutral buoyancy.

3. Error due to variations in seawater density

The range of seawater temperature and salinities likely to be encountered by an elephant seal from Macquarie Island corresponds to a seawater density range of 1.027 – 1.030 g/cm³. This represents about 2.5 % of the range of densities for seals over the range of lipid contents (0.982 – 1.100 g/cm³), and would result in a maximum error in predicted lipid content of 1.3 % (Figure 7d).

Model evaluation

1. Simulation test

Our sensitivity analysis indicated that the prediction accuracy was highly dependent on which parameters were kept constant and which were randomly selected from the pre-defined probability distributions. When all parameter values were randomly selected, 95% of the residuals of predicted vs. actual lipid contents were between –7.3 and 6.4 % lipid (Table 2). When seawater density was kept constant at 1028 g/m² while allowing all other parameters to vary, this error range was reduced by only about 0.5 %. The error reduction was slightly larger when we kept body surface area and volume constant while allowing all other parameters to vary (error reduction ~5.8 %). The most dramatic reduction in prediction errors was achieved when the C_D was kept constant at 0.83, resulting errors ranging from about –2.6 to 1.8 % lipid. Our

results indicate that while uncertainties in seawater density and body surface area and volume together are not likely to result in prediction errors of more than about ± 2.5 %, uncertainties in C_D can cause errors in lipid content of over 10 %. Furthermore, the errors were highly dependent on the magnitude of positive or negative drift rate. The smallest errors were calculated for drift rates around zero while errors increased towards the extremes of the range of our data.

Parameter kept constant	Lower 95%	Mean	Upper 95%	Range	Error range reduction (%)
None	-7.30	-0.22	6.43	13.72	
Seawater density	-7.03	-0.01	6.62	13.65	0.52
Surface area & volume	-6.64	-0.21	6.29	12.93	5.79
Drag coefficient	-2.65	-0.20	1.80	4.45	67.54

Table 2. Results from the simulation analysis of the relative importance of errors in surface area and volume, seawater density and C_D on the prediction errors of lipid content from drift rates (see text and legend for Figure 9 for further details). Values in the first four columns represent percent lipid content, while values in the last column represent the percent reduction in the 95% error range relative to the error range when no parameters were kept constant (i.e. $100 \times (13.65/13.72) = 0.52$).

2. Correlation between predicted and measured lipid content

Due to lack of body composition measurements and/or lack of drift dives early in the record, twelve seals were excluded from the following comparison. Table 3 presents data from the remaining twelve seals for which data were sufficient. There was a strong positive correlation between predicted and measured lipid contents using either of the two criteria used (see methods; i.e. the “minimum sum of squared residuals” criterion or the “Slope = 1” criterion) for finding the optimal C_D value.

REF	Departure lipid content (%)				Minimum lipid content (%)				
	Minimum error		Slope = 1		Minimum error		Slope = 1		
	Measured	Predicted	Residual	Predicted	Residual	Predicted	Residual	Predicted	Residual
2846_99	43.29	36.28*	7.01*	36.45*	6.84*	29.06	31.18	77	137
28497_99	37.18	42.14*	-4.97*	53.31*	-16.13*	24.16	27.70	38	84
28496_99	42.12	40.07	2.05	38.99	3.13	30.15	31.95	93	152
26627_99	43.15	34.78*	8.37*	36.07*	7.08*	25.27	28.49	27	76
28494_99	42.51	41.37	1.15	40.5	2.01	32.69	33.76	24	82
17217_99	41.79	41.83	-0.04	40.24	1.55	29.25	31.31	42	106
2849_99	41.04	39.21	1.83	37.99	3.05	30.01	31.85	58	121
5812_99	40.63	39.53	1.10	39.07	1.56	25.07	28.34	57	98
Cleo_00	39.81	40.48	-0.67	39.29	0.52	28.41	30.72	42	114
FirstOne_00	23.1	25.56*	2.46*	28.53*	-5.43*	23.34	27.11	57	87
Ella_00	45.81	41.25*	4.56*	43.37*	2.44*	26.61	29.44	41	101
Alice_00	41.78	43.88	-2.10	41.7	0.08	27.01	29.72	63	123
Flora_00	46.19	43.53	2.66	43.41	2.78	30.62	32.28	65	126
Billie_00	39.37	37.9	1.47	38.57	0.8	26.24	29.18	100	152
Doris_00	42.54	40.61	1.93	39.38	3.16	28.99	31.12	36	87
20918_00	43.28	43.54	-0.26	41.46	1.82	24.75	28.12	32	76
Mean	40.85	41.09	1.39 ⁰	40.05	1.86	27.60	30.14	53.25	107.63
SD	5.24	1.95	0.82 ⁰	1.61	1.09	2.68	1.90	22.42	25.56
Min	23.10	37.90	-2.10	37.99	0.08	23.34	27.11	24	76
Max	46.19	43.88	2.66	43.41	3.16	32.69	33.76	100	152

Table 3. Correlation between lipid contents at departure measured using the labelled water method and lipid contents at the start of the SRDL record predicted using the C_D of a sphere (0.49). "Residual" refer to the difference between the actual and the predicted lipid content. "Day after" refers to how many days after weaning and departure measurements were done. "Minimum lipid content" refers to the lowest predicted lipid content observed, and "Day after" again refer to the number of days after departure and weaning when this minimum occurred. Brackets and an asterisk indicate values that were excluded from summary statistics and correlation analysis for reasons described in the text and in the legend for Figure 9. The mean and standard deviations for the residuals were calculated based on the absolute difference between predicted and measured lipid contents. Summary statistics marked with a ⁰ were calculated from absolute residuals, and values marked with an asterisk were excluded from the summary statistics (see text for further details).

Minimum sum of squared residuals criterion: The minimum sum of squared residuals (SSR) was obtained using a C_D of 0.69 (SSR = 19.03, Fig 8). Using this C_D , the mean absolute difference between predicted and measured lipid contents was 1.39 % (Table 3). The slope of the linear regression of measured against predicted drift rates was less than 1 ($PTBF_{Measured} = 0.71(PTBF_{Predicted}) + 12.37$, $F_{1;10} = 29.69$, $R^2 = 0.72$), but the deviation from a slope of unity was not quite significant at the 0.05 level (t-test, $t = -2.20$, $p = 0.052$). Lipid contents predicted from drift dives were underestimated for leaner seals compared to the measured lipid contents, while they were overestimated for fatter seals (Fig 9).

Slope = 1 criterion: We obtained a slope coefficient of 1 using a C_D of 0.49 ($PTBF_{Measured} = PTBF_{Predicted} + 1.80$, $F_{1;10} = 29.69$, $R^2 = 0.72$, Fig 8). This C_D resulted in predicted lipid contents that were on average 1.86 % lower than those measured using labelled water (Table 3), and because the slope was one, this bias was constant throughout the range of lipid contents (Fig 9).

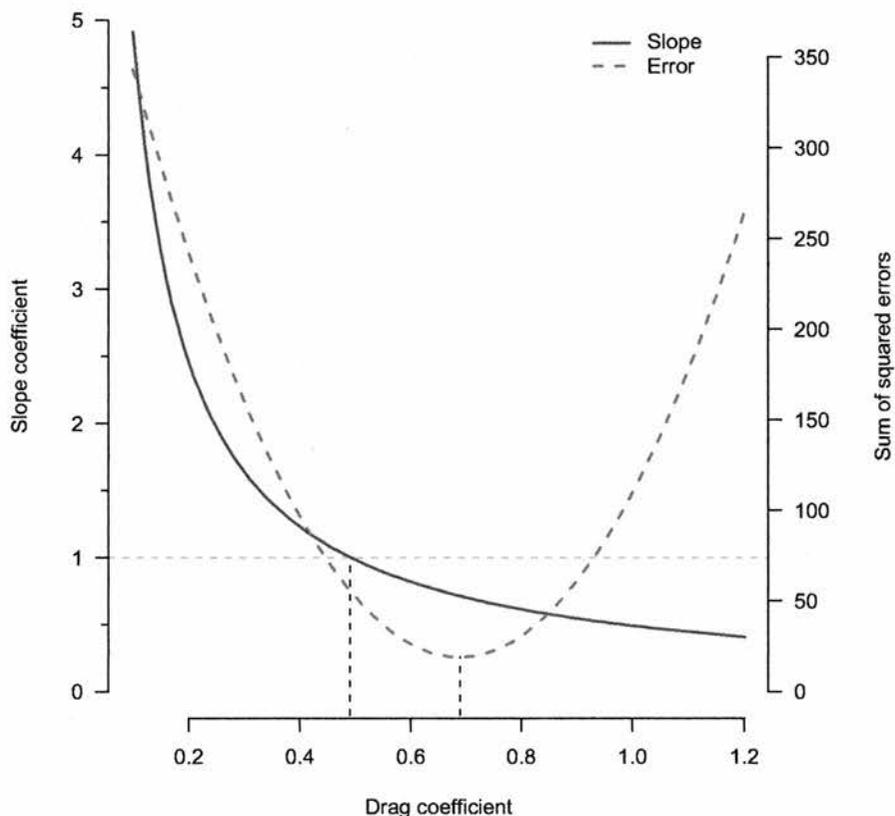


Figure 8. Regression slope coefficient and sum of squared residuals between predicted and measured lipid contents expressed as functions of drag coefficients (C_D) (ranging from 0.09 to 1.20) used in the predictive model of lipid content. The red line represents the sum of squared residuals (SSR) for each C_D value used, while the blue line represents the slope coefficient. The horizontal dotted line represents a slope coefficient of 1, and the left-hand vertical dotted line represents the corresponding C_D value (0.49). The right-hand vertical dotted line represents the C_D value (0.69) that corresponded to the minimum sum of squared residuals of predicted and measured lipid contents (see also Figure 9).

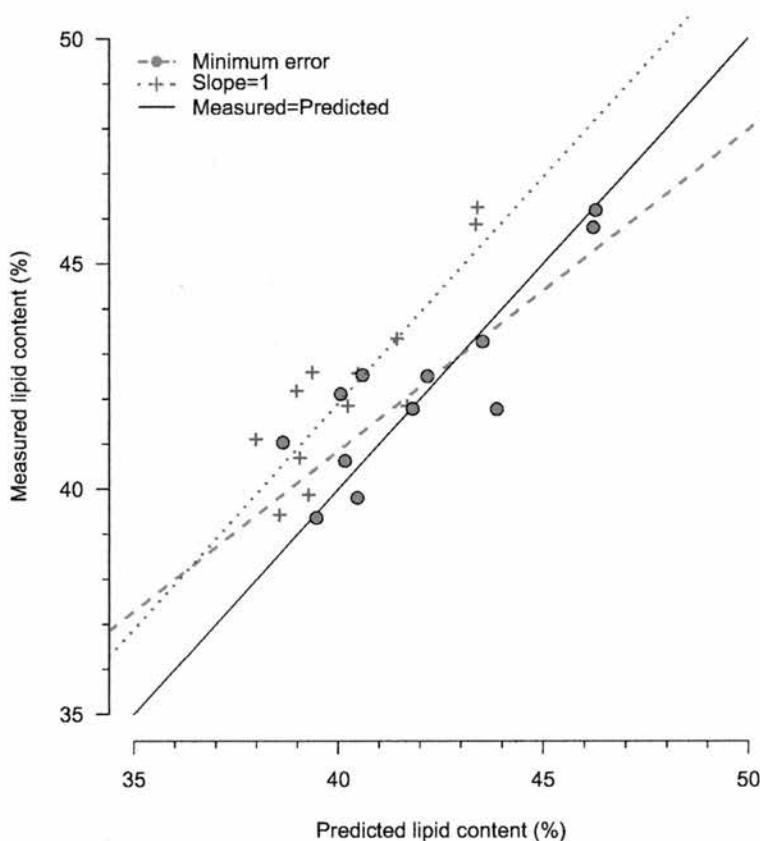


Figure 9. Correlation between lipid content at the start of the trip predicted from the fitted drift rates at departure (using the fitted spline function) for each individual seal, and the lipid content measured just prior to departure using the labelled water method. The solid thick line represents predicted lipid contents being identical to the measured lipid contents. The red points (each point representing an individual seal) were obtained using the drag coefficient (CD) that minimised the sum of squared residuals between predicted and measured values ($CD = 0.69$), while the blue crosses (again, each cross representing one individual seal) represent the analysis using a CD value that produced a regression slope of unity ($CD = 0.49$, see text and Figure 8). The regression lines for these two models are represented by the red and blue dotted lines respectively (see text for regression results). Individuals for which the first daily fitted drift rate (and predicted lipid content) occurs more than 10 days after departure (20918_99, 28497_99 and 28504_99, see Table 3), and/or for which the initial fitted drift rate (and predicted lipid content) is calculated from one isolated drift dive early in the record followed by a long gap in the data (2846_99 and 26627_99), were excluded from the graph and the analysis. Also, one individual (FirstOne_00) for whom the drift dive record shows an unusual pattern and is probably subject to significant dive misclassifications, have also been excluded.

Using the drag coefficients obtained using the two criteria, we estimated the lipid content of each seal when this had reached its minimum value, i.e. at the transition between Phase 1 and 2 (Table 3). Using the “minimum SSR” criterion ($C_D = 0.69$), the predicted lipid contents ranged from 23.3 to 32.7 % (mean = 27.6 %), while the “Slope = 1” criterion gave a higher average (30.1 %) but a smaller range (27.1 – 33.8 %). but the lowest predicted values generally occurred within ~ 30 – 80 days after departure, or ~ 80 – 150 days after weaning, but varied substantially between individuals (Table 3).

Discussion

In this study we have demonstrated how drift dives can be used to estimate the body composition of free-ranging elephant seals. This idea has been proposed before (e.g. Crocker et al., 1997; Webb et al., 1998), but our study expands these ideas and presents a quantitative analysis of the influence of various assumptions and potential sources of error and bias. The method makes use of simple dive characteristics, as recorded by readily available data logging and telemetry instruments, and therefore does not require the use of specialized sensors. If the recorded data are transmitted via satellite, the method also allows us to monitor the changes in body composition as they occur, even in animals that do not return to a place where they can be recaptured and measured. The cause of a particular change in relative body composition may not always be known (i.e. an increase in relative lipid content may occasionally be a result of selective protein depletion rather than lipid assimilation; see discussion below), but this method may nevertheless provide important clues about the spatial and temporal distribution of foraging. Although drift dives have so far only been documented for

elephant seals, other species may display dive characteristics that can be used in a similar way to estimate body condition.

General temporal changes in drift rate

The general division of the trips into three phases based on the first and last days of positive change in drift rate agreed well with the transition days based on the travel rate threshold used by e.g. Le Boeuf et al. (2000) and McConnell et al. (2002) (Figures 3 and 4). Our data suggest that the initial 30 – 50 day period is characterised by relatively high travel rates and a gradual decrease in buoyancy, presumably as a result of depletion of onboard lipid stores. The switch from a decrease to an increase in buoyancy is not abrupt, and this is followed by a longer period (~100 days) of overall increase in drift rate and buoyancy caused by increasing lipid stores. While some individuals show a gradual increase in drift rate and buoyancy, others appear to go through cycles of energy gain and energy loss (Figure 4). These cycles of increase and decrease in drift rate are sometimes correlated with travel rate, possibly reflecting seals moving between profitable prey patches. At other times seals appear to be in negative energy balance despite slow travel rates (Figure 4 & 7), possibly reflecting seals foraging in less profitable patches. During the last phase there was again a slight decrease in drift rate and buoyancy while seals were in transit back to the island.

The correspondence between travel rate and change in drift rate is not perfect, and there often appears to be a time lag between changes in travel rate and changes in drift rate. For instance, the ingestion of a prey item may not necessarily be followed by an immediate positive change in drift rate. Although lipid from prey may be assimilated into the blubber tissue relatively rapidly, the excretion of residual material as faeces

may take longer. These residual materials are likely to be of similar or higher density than that of seawater, and may result in a decreased overall buoyancy of the animal. However, captive studies on juvenile southern elephant seals indicate that the passage rate of faecal matter is on the order of 10-20 hours (Krockenberger and Bryden, 1994), and the delay between prey assimilation and increased buoyancy caused by this factor is therefore unlikely to be significant over greater time scales.

The time lags between changing daily travel rates and daily change in drift rate may occasionally be the result of sampling errors. For instance, the daily travel rates have been calculated from Argos locations, which are subject to error (e.g. Vincent et al., 2002). However, we expect these errors to be relatively insignificant in relation to the distances covered by southern elephant seals, especially since we have used daily locations based on averaging over several location fixes.

Mechanistic model and sources of error

Drag, buoyancy and drift rate: The sigmoid shape of the relationship between lipid content and predicted drift rate has important implications for using drift rate to predict body composition. For animals close to neutral buoyancy, a small change in body composition (and thus buoyant force) will cause a large change in drift rate, while an equivalent change will result in a smaller change in drift rate for fatter and leaner seals. We may therefore expect smaller prediction errors in body composition around a drift rate of zero, while these errors should increase towards both extremes of drift rate and lipid content.

Surface area and volume: For animals like elephant seals that perform extended foraging trips lasting several months, and that have a life history characterized by dramatic cycles of fasting and feeding, the surface area and body volume is likely to change significantly over the course of the trip. This is particularly true in the case of juvenile animals that grow continuously during the time spent at sea. These changes will influence the drag resistance as well as the buoyancy, and may lead to errors in our predictions of body composition from the observed drift rates. Because drag is directly proportional to the surface area, errors in our estimates of this area will have greater influence on our lipid content predictions towards the extremes of drift rate and lipid content, whereas these errors should approach zero when the buoyancy approaches neutral. However, based on all seals measured before and after this first foraging trip (SMRU, unpublished data) surface area for an average seal is estimated to change from $\sim 0.8 \text{ m}^2$ at departure to $\sim 1.1 \text{ m}^2$ at return. For a seal with an average body composition ($\sim 25\text{-}35 \%$ lipid), this would correspond to an error in predicted lipid content of no more than $\sim 2 \%$. This is further supported by our simulation analyses, which suggest that errors in estimated surface area and volume contribute only slightly to the overall prediction errors (Table 2).

Residual air: As illustrated in Figure 7 (a and b), residual air in the lungs can have a significant influence on our predictions of body composition, and this bias will depend on the depth over which the drift segment occurs. Again, for an observed drift rate of -23 cm/s we would predict a lipid content of $\sim 27 \%$ if residual air is not accounted for, while the actual lipid content would be about 14, 23 and 25 % if the drift rate was measured at 10, 50 and 100 m depth respectively. This prediction bias can either be reduced, by excluding dives shallower than a specified depth (e.g. $\sim 4 \%$

and 2% bias when excluding all dives <50 and <100 m respectively), or the bias can be controlled for by estimating the residual lung volume for a given individual at a representative depth of each dive (e.g. a depth halfway between the start and end depths of the drift segment). We should also point out that seals in this study showed a greater variability in drift rate during shallow dives (<100m) compared to deeper dives. This may be a result of seals voluntarily adjusting the volume of residual air to optimise buoyancy during shallow dives. This effect would obviously disappear at greater depths due to the exponential decrease in air volume by depth, reducing the variability in drift rate. Minamikawa et al. (2000) showed that loggerhead turtles perform dives during which they remain at a particular depth without actively swimming, and select the depth in order to maintain neutral buoyancy. Although this so-called “residence depth” is affected by the amount of air in the lungs, turtles did not appear to actively determine this depth by adjusting the amount of air. However, Sato et al. (2002b) argue that king (*Aptenodytes patagonicus*) and adelic (*Pygoscelis adeliae*) penguins voluntarily regulate the air volume at the start of a dive depending on the expected duration of the dive, in order to optimise the costs and benefits of buoyancy.

Seawater density: Although elephant seals perform long migrations and deep dives, crossing many sharp temperature and salinity gradients, the maximum range in seawater density encountered by seals in this study is very small in relation to the variations in body density, and our simulation tests showed that errors in seawater density account for only a small proportion (< 1%) of the overall errors (Table 2 and Figure 7d).

Drag coefficient: Our simulation tests indicate that C_D was the most important factor contributing to the overall uncertainty in predicted lipid content (Table 2), even though the range of C_D s in this analysis were limited to values between 0.47 (sphere) and 1.17 (cylinder). Our previous analyses (see Figure 6) suggest that C_D values of the magnitude observed for various streamlined objects (including fish and marine mammals) at similar Reynolds numbers ($C_D \sim 10^{-4} - 10^{-2}$ (Vogel, 1981)) are unrealistic, and we consequently excluded C_D values smaller than that of a sphere (0.47) from this analysis.. Randomly selecting the C_D from values between that of a sphere and that of a cylinder accounted for over 90 % of the total error attributed by surface area & volume, seawater density and C_D combined.

Predicted and actual lipid content

There was a strong correlation between lipid content predicted using drift rates and the lipid content estimated using labelled water (Figure 9). When volume, surface area and residual air volume were estimated from morphometric measurements prior to departure we were able to estimate lipid content at the start of the trip to within a few percent (Table 3). We were also able to obtain a good estimate of the most likely range of drag coefficients by allowing this to be fitted as a parameter by the model. Our results suggest that, while drifting passively through the water column, the C_D of our seals was ~ 0.49 (using the “Slope = 1” criterion) – 0.69 (using the “minimum SSR” criterion). At Reynolds numbers between 10^4 to 10^6 , the C_D of a sphere is ~ 0.47 (see above), while a prolate spheroid travelling crosswise has a C_D of ~ 0.59 . It is important to emphasize that we should not expect C_D to be constant. The drag force acting on animals is likely to vary as a result of postural changes in response to perceived conditions, and this could have a confounding affect on the interpretation of

buoyancy data. However, if drift dives are indeed resting dives, as was proposed by Crocker et al. (1997), it would make sense for a seal to minimise its vertical movement while remaining passive. This could be accomplished by using the flippers as brakes or trim tabs. Such behavioural adjustments would further increase the drag force, and may explain the discrepancy between the C_D value for a prolate spheroid (~ 0.59) and our upper estimate (0.69).

Although our analyses have provided a good estimate of C_D for a phocid drifting passively in a direction different from that of normal travel (headfirst) further experiments in the laboratory and in the field may improve our understanding of this behaviour. For instance, the C_D of a seal or seal-like body moving at different angles relative to the surrounding fluid could be measured in the lab where these angles as well as the speed can be controlled. Another promising development is that of accelerometer loggers that can be attached to animals to measure swimming activity and body orientation. These instruments have already been used to identify fine-scale movements such as so-called “burst-and-glide” swimming in free ranging cetaceans, seals and penguins (e.g. Nowacek et al., 2001; Sato et al., 2002b). Sato et al. (2003) also measured the swimming activity and body orientation of free-ranging Weddell seals, and found that while fatter seals predominantly showed “burst-and-glide” swimming on descent, leaner seals were able to glide throughout most of this descent phase. These findings suggest that it may be possible to monitor changes in body composition of seals that do not regularly perform drift dives. Other indices may be used, such as the depth at which seals stop flipper beating on descent, the ratio of burst to glide periods, or the rate of deceleration of a seal after each burst.

Although such experiments would improve the technique, our simple model still allowed us to make some inferences about changes in body composition of seals while at sea. At the start of their first trip, after the ~ 5 – 8 week post-weaning fast on land (SMRU unpublished data), the fattest individuals had a measured lipid content almost twice that of the leanest seals (range: ~ 23 - 46 %, Table 3). Our model estimated that seals reduced their relative lipid content by between about 7 and 20 % during the first ~50 days of the trip, and that the lipid content at the transition between phase 1 and 2 was ~ 23 – 33 % (Table 3). McConnell et al. (2002) estimated the time to protein and fat starvation for southern elephant seal pups using measurements of mass loss and changes in body composition during the post-weaning fast on land (Arnbom et al., 1993; Carlini et al., 2001), assuming that the metabolic rate was similar at sea and on land. They estimated the average time to protein and fat starvation respectively as 70.2 and 77.9 days for small (light) seals, and 81.1 and 113.8 days respectively for large (heavy) seals, and suggested that while light seals would have reached critical levels at the end of phase 1 (defined using the travel rate criterion), heavy seals would still be in relatively good condition at this transition. These estimates are generally lower than the ~80 – 150 days between weaning and the occurrence of the minimum lipid content estimated from drift rates in this study (Table 3). However, the changes in drift rate indicate that the change from negative to positive energy balance was not abrupt. Instead, the rate of negative change started declining around 25 – 30 days after departure (roughly 60 – 100 days after weaning) (Figures 4 & 6, Table 1), and even at the time of minimum drift rate (and lipid content), all our seals still appeared to have sufficient energy reserves (i.e. a lipid content of ~23 – 33 % compared to the estimated critical level of 10% (Cahill et al., 1979; McConnell et al., 2002). This may indicate that most pups start feeding gradually while still in transit, thereby reducing

their rates of energy depletion and avoid reaching critical levels. It is also possible that seals have a suppressed metabolic rate while at sea compared to when resting on land (Hindell and Lea, 1998), and that the times to fat and protein starvation in McConnell et al. (2002) are slightly underestimated.

Conclusion

To our knowledge this is the first time changes in body composition of free-ranging phocids have been estimated at sea. We have demonstrated that a thorough analysis of drift rate is a valuable tool for monitoring the changes in body composition of free ranging marine animals, and can be used to predict body composition to within a few percent. Our model also allowed us to estimate the minimum body composition of seals at the end of the transit from the island to their foraging grounds. Our estimates suggest that the energy stores of these naïve seal pups are unlikely to approach critically low levels before the onset of feeding. We believe that this approach is a valuable extension to the current use of data recorders and telemetry, and that it has the potential of providing more accurate and finer resolution data on important feeding areas and seasons for large marine predators, and may therefore be used as a basis for more informed management decisions for species exploiting distant areas of the oceans over long time periods.

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References

- Argos. (1989). Guide to the Argos System. Toulouse: Argos CLS.
- Arnborn, T., Fedak, M. A., Boyd, I. L. and McConnell, B. J. (1993). Variation in Weaning Mass of Pups in Relation to Maternal Mass, Postweaning Fast Duration, and Weaned Pup Behavior in Southern Elephant Seals (*Mirounga Leonina*) At South-Georgia. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 71, 1772-1781.
- Beck, C. A., Bowen, W. D. and Iverson, S. J. (2000). Seasonal changes in buoyancy and diving behaviour of adult grey seals. *Journal of Experimental Biology* 203, 2323-2330.
- Bekkby, T. and Bjorge, A. (1998). Variation in stomach temperature as indicator of meal size in harbor seals, *Phoca vitulina*. *Marine Mammal Science* 14, 627-637.
- Bell, W. J. (1991). Searching behaviour - The behavioural ecology of finding resources. London: Chapman and Hall.
- Bost, C. A., Georges, J. Y., Guinet, C., Cherel, Y., Putz, K., Charrassin, J. B., Handrich, Y., Zorn, T., Lage, J. and LeMaho, Y. (1997). Foraging habitat and food intake of satellite-tracked king penguins during the austral summer at Crozet Archipelago. *Marine Ecology-Progress Series* 150, 21-33.
- Boyd, I., Arnborn, T. and Fedak, M. (1993). Water Flux, Body-Composition, and Metabolic-Rate During Molt in Female Southern Elephant Seals (*Mirounga Leonina*). *Physiological Zoology* 66, 43-60.
- Boyd, I. L. and Arnborn, T. (1991). Diving Behavior in Relation to Water Temperature in the Southern Elephant Seal - Foraging Implications. *Polar Biology* 11, 259-266.
- Cahill, G. F., Marliss, E. B. and Aoki, T. T. (1979). Fat and nitrogen metabolism in fasting man. *Hormone Metab.Res.* 2, 181-185.
- Carlini, A. R., Márquez, M. E. I., Ramdohr, S., Bornemann, H., Panarello, H. O. and Daneri, G. A. (2001). Postweaning Duration and Body Composition Changes in Southern Elephant Seal (*Mirounga leonina*) Pups at King George Island. *Physiological and Biochemical Zoology* 74, 531-540.
- Chappell, M. A., Shoemaker, V. H., Janes, D. N., Maloney, S. K. and Bucher, T. L. (1993). Energetics of Foraging in Breeding Adelie Penguins. *Ecology* 74, 2450-2461.
- Charrassin, J. B., Kato, A., Handrich, Y., Sato, K., Naito, Y., Ancel, A., Bost, C. A., Gauthier-Clerc, M., Ropert-Coudert, Y. and Le Maho, Y. (2001). Feeding behaviour of free-ranging penguins determined by oesophageal temperature. *Proceedings of the Royal Society of London Series B-Biological Sciences* 268, 151-157.
- Crocker, D. E., Le Boeuf, B. J. and Costa, D. P. (1997). Drift diving in female northern elephant seals: Implications for food processing. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 75, 27-39.
- Davis, R. W., Fuiman, L. A., Williams, T. M., Collier, S. O., Hagey, W. P., Kanatous, S. B., Kohin, S. and Horning, M. (1999). Hunting behaviour of a marine mammal beneath the Antarctic fast ice. *Science* 283, 993-996.
- Fancy, S. G., Pank, L. F., Douglas, D. C., Curby, C. H., Garner, G. W., Amstrup, S. C. and Regelin, W. L. (1988). Satellite telemetry: A new tool for wildlife

- research and management. U.S. Department of the Interior, U.S. Fish and Wildlife Service resource Publication 172.
- Fedak, M., Lovell, P., McConnell, B. and Hunter, C. (2002). Methods for overcoming the constraints of long range telemetry of biological information from animals: getting more useful data from small packages. *Integrative and Comparative Biology* 42, 3-10.
- Fedak, M. A. (1992). Real-time telemetry techniques: Observing the behaviour and physiology of seals at sea with VHF and acoustic telemetry.
- Fedak, M. A., Anderson, S. S. and Curry, M. G. (1983). Attachment of a radio tag to the fur of seals. *Journal of Zoology* 200, 298-300.
- Fedak, M. A., Lovell, P. and Grant, S. M. (2001). Two approaches to compressing and interpreting time-depth information as collected by timed-depth recorders and satellite linked data loggers. *Marine Mammal Science* 17, 94-110.
- Field, I. C., Bradshaw, C. J. A., McMahan, C. R., Harrington, J. and Burton, H. R. (2002). The effects of multiple anaesthesia in using tiletamine and zolasepam on Southern elephant seals (*Mirounga leonina*) at Macquarie Island. *Veterinary Record*.
- Gales, R. and Renouf, D. (1993). Detecting and Measuring Food and Water-Intake in Captive Seals Using Temperature Telemetry. *Journal of Wildlife Management* 57, 514-519.
- Garthe, S., Gremillet, D. and Furness, R. W. (1999). At-sea-activity and foraging efficiency in chick-rearing northern gannets *Sula bassana*: a case study in Shetland. *Marine Ecology-Progress Series* 185, 93-99.
- Georges, J. Y., Bonadonna, F. and Guinet, C. (2000). Foraging habitat and diving activity of lactating Subantarctic fur seals in relation to sea-surface temperatures at Amsterdam Island. *Marine Ecology-Progress Series* 196, 291-304.
- Gordon, A. L. (1988). Spatial and temporal variability within the Southern Ocean. In *Antarctic Ocean and resources variability*, (ed. D. Sahrhage), pp. 41-56. Berlin: Springer Verlag.
- Gu and Wahba. (1991). Minimizing GCV/GML scores with multiple smoothing parameters via the Newton method. *SIAM J. Sci. Statist. Comput.* 12, 383-398.
- Guinet, C., Dubroca, L., Lea, M. A., Goldsworthy, S., Cherel, Y., Duhamel, G., Bonadonna, F. and Donnay, J. P. (2001). Spatial distribution of foraging in female Antarctic fur seals *Arctocephalus gazella* in relation to oceanographic variables: a scale-dependent approach using geographic information systems. *Marine Ecology-Progress Series* 219, 251-264.
- Hedd, A., Gales, R. and Renouf, D. (1996). Can stomach temperature telemetry be used to quantify prey consumption by seals? A re-examination. *Polar Biology* 16, 261-270.
- Hindell, M. A. and Lea, M. A. (1998). Heart rate, swimming speed, and estimated oxygen consumption of a free-ranging southern elephant seal. *Physiological Zoology* 71, 74-84.
- Hindell, M. A., McConnell, B. J., Fedak, M. A., Slip, D. J., Burton, H. R., Reijnders, P. J. H. and McMahan, C. R. (1999). Environmental and physiological determinants of successful foraging by naive southern elephant seal pups during their first trip to sea. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 77, 1807-1821.

- Hindell, M. A., McConnell, B. J., Slip, D. J., Fedak, M. A., Burton, H. R. and Reijnders, P. J. H. (1998). Diving behaviour in newly-weaned southern elephant seals during their first trip to sea.
- Hooker, S. K., Boyd, I. L., Jessopp, M., Cox, O., Blackwell, J., Boveng, P. L. and Bengtson, J. L. (2002). Monitoring the prey-field of marine predators: Combining digital imaging with datalogging tags. *Marine Mammal Science* 18, 680-697.
- Ihaka, R. and Gentleman, R. (1996). R: A language for data analysis and graphics. *Journal of Computational and Graphical Statistics* 5, 299-314.
- Klimley, A. P., Le Boeuf, B. J., Cantara, K. M., Richert, J. E., Davis, S. F., Van Sommeran, S. and Kelly, J. T. (2001). The hunting strategy of white sharks (*Carcharodon carcharias*) near a seal colony. *Marine Biology* 138, 617-636.
- Koenker, R. W. and Bassett, G. W. (1978). Regression quantiles. *Econometrica* 46, 33-50.
- Kooyman, G. L. (1965). Techniques used in measuring diving capacities of Weddell seals. *Polar Record* 12, 391-394.
- Kooyman, G. L. (1989). *Diverse Divers: physiology and behaviour*. Berlin: Springer-Verlag.
- Kooyman, G. L., Cherel, Y., Lemaho, Y., Croxall, J. P., Thorson, P. H. and Ridoux, V. (1992). Diving Behavior and Energetics During Foraging Cycles in King Penguins. *Ecological Monographs* 62, 143-163.
- Krockenberger, M. B. and Bryden, M. M. (1994). Rate of Passage of Digesta Through the Alimentary-Tract of Southern Elephant Seals (*Mirounga-Leonina*) (Carnivora, Phocidae). *Journal of Zoology* 234, 229-237.
- Le Boeuf, B. J., Crocker, D. E., Costa, D. P., Blackwell, S. B., Webb, P. M. and Houser, D. S. (2000). Foraging ecology of northern elephant seals. *Ecological Monographs* 70, 353-382.
- Le Boeuf, B. J., Naito, Y., Asaga, T., Crocker, D. and Costa, D. P. (1992). Swim Speed in a Female Northern Elephant Seal - Metabolic and Foraging Implications. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 70, 786-795.
- Lesage, V., Hammill, M. O. and Kovacs, K. M. (1999). Functional classification of harbor seal (*Phoca vitulina*) dives using depth profiles, swimming velocity, and an index of foraging success. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 77, 74-87.
- Lovvorn, J. R. and Jones, D. R. (1991a). Body mass, volume, and bouyancy of some aquatic birds, and their relation to locomotor strategies. *Canadian Journal of Zoology* 69, 2888-2892.
- Lovvorn, J. R. and Jones, D. R. (1991b). Effects of body size, body fat, and change in pressure with depth on buoyancy and costs of diving in ducks (*Aythya* spp.). *Canadian Journal of Zoology* 69, 2879-2887.
- McConnell, B. J. (1986). Tracking grey seals using service ARGOS. *Mesogee* 46, 93-94.
- McConnell, B. J., Fedak, M. A., Burton, H. R., Englehard, G. H. and Reijnders, P. (2002). Movements and foraging areas of naive, recently weaned southern elephant seal pups. *Journal of Animal Ecology* 71, 65-78.
- McMahon, C. R., Burton, H., McLean, S., Slip, D. and Bester, M. (2000a). Field immobilisation of southern elephant seals with intravenous tiletamine and zolazepam. *Veterinary Record* 146, 251-254.

- McMahon, C. R., Burton, H. R. and Bester, M. N. (2000b). Weaning mass and the future survival of juvenile southern elephant seals, *Mirounga leonina*, at Macquarie Island. *Antarctic Science* 12, 149-153.
- Minamikawa, S., Naito, Y., Sato, K., Matsuzawa, Y., Bando, T. and Sakamoto, W. (2000). Maintenance of neutral buoyancy by depth selection in the loggerhead turtle *Caretta caretta*. *Journal of Experimental Biology* 203, 2967-2975.
- Moore, F. D., Olsen, K. H., McMurray, J. D., Parker, H. V., Ball, M. R. and Boyden, C. M. (1963). The body cell mass and its supporting environment: body composition in health and disease. Philadelphia: W. B. Saunders.
- Nagy, K. A. and Costa, D. P. (1980). Water flux in animals: analysis of potential errors in the tritiated water method. *Am. J. Physiol.* 238, R454-R465.
- Nowacek, D. P., Johnson, M. P., Tyack, P. L., Shorter, K. A., McLellan, W. A. and Pabst, D. A. (2001). Buoyant balaenids: the ups and downs of buoyancy in right whales. *Proceedings of the Royal Society of London Series B-Biological Sciences* 268, 1811-1816.
- Putz, K. and Bost, C. A. (1994). Feeding-Behavior of Free-Ranging King Penguins (*Aptenodytes- Patagonicus*). *Ecology* 75, 489-497.
- Putz, K., Wilson, R. P., Charrassin, J. B., Raclot, T., Lage, J., Le Maho, Y., Kierspel, M. A. M., Culik, B. M. and Adelung, D. (1998). Foraging strategy of King Penguins (*Aptenodytes patagonicus*) during summer at the Crozet Islands. *Ecology* 79, 1905-1921.
- Reilly, J. J. and Fedak, M. A. (1990). Measurement of the Body-Composition of Living Gray Seals By Hydrogen Isotope-Dilution. *Journal of Applied Physiology* 69, 885-891.
- Sato, K., Mitani, Y., Cameron, M. F., Siniff, D. B. and Naito, Y. (2003). Factors affecting stroking patterns and body angle in diving Weddell seals under natural conditions. *Journal of Experimental Biology* 206, 1461-1470.
- Sato, K., Mitani, Y., Cameron, M. F., Siniff, D. B., Watanabe, Y. and Naito, Y. (2002a). Deep foraging dives in relation to the energy depletion of Weddell seal (*Leptonychotes weddellii*) mothers during lactation. *Polar Biology* 25, 696-702.
- Sato, K., Naito, Y., Kato, A., Niizuma, Y., Watanuki, Y., Charrassin, J. B., Bost, C. A., Handrich, Y. and Le Maho, Y. (2002b). Buoyancy and maximal diving depth in penguins: do they control inhaling air volume? *Journal of Experimental Biology* 205, 1189-1197.
- Schreer, J. F. and Testa, J. W. (1996). Classification of Weddell seal diving behavior. *Marine Mammal Science* 12, 227-250.
- Tanaka, H., Sato, K., Matsuzawa, Y., Sakamoto, W., Naito, Y. and Kuroyanagi, K. (1995). Analysis of Possibility of Feeding of Loggerhead Turtles During Internesting Periods Based On Stomach Temperature-Measurements. *Nippon Suisan Gakkaishi* 61, 339-345.
- Venables, W. N. and Ripley, B. D. (1994). Modern applied statistics with S-plus. New York: Springer-Verlag.
- Vincent, C., McConnell, B., Ridoux, V. and Fedak, M. (2002). Assessment of Argos location accuracy from satellite tags deployed on captive grey seals. *Marine Mammal Science* 18, 156-166.
- Vogel, S. (1981). Live in moving fluids. Boston: Willard Grant Press.
- Webb, P. M., Crocker, D. E., Blackwell, S. B., Costa, D. P. and Le Boeuf, B. J. (1998). Effects of buoyancy on the diving behavior of northern elephant seals. *Journal of Experimental Biology* 201, 2349-2358.

- Weimerskirch, H. and Wilson, R. P. (1992). When do wandering albatrosses *Diomedea exulans* forage? *Marine Ecology - Progress Series* 86, 297-300.
- Williams, T. M. and Kooyman, G. L. (1985). Swimming performance and hydrodynamic characteristics of harbor seals *Phoca vitulina*. *Physiological Zoology* 58, 576-589.
- Wilson, R., Peters, G., Regel, J., Gremillet, D., Putz, K., Kierspel, M., Weimerskirch, H. and Cooper, J. (1998). Short retention times of stomach temperature loggers in free-living seabirds: is there hope in the spring? *Marine Biology* 130, 559-566.
- Wilson, R. P. (1992). Environmental Monitoring With Seabirds - Do We Need Additional Technology. *South African Journal of Marine Science-Suid-Afrikaanse Tydskrif Vir Seewetenskap* 12, 919-926.
- Wilson, R. P., Putz, K., Gremillet, D., Culik, B. M., Kierspel, M., Regel, J., Bost, C. A., Lage, J. and Cooper, J. (1995). Reliability of Stomach Temperature-Changes in Determining Feeding Characteristics of Seabirds. *Journal of Experimental Biology* 198, 1115-1135.

CHAPTER 4: ACHIEVING AUTONOMY: BODY COMPOSITION, ENERGY BUDGETS AND SURVIVAL OVER THE FIRST YEAR

Abstract

The short but intensive lactation period in most phocids is terminated abruptly when mothers return to sea to feed, and pups remain on land fasting for several weeks before they too embark on their first foraging trip. It is crucial for a pup to allocate and utilise its finite resources to balance immediate energetic and behavioural demands with the probability of finding food within a given time. Previous research on southern and northern elephant seals has described the energetics and condition of pups during the initial fast on land. In this chapter we describe individual variation and changes in size and body condition of Southern elephant seal pups over the first and second trip to sea during their first year of life. We also examine the effects of body condition on haulout patterns and survival of individuals.

While overall and lean body mass increased linearly throughout the year, there were large variations in the assimilation of lipid energy reserves. While some seals returned for the midyear winter haulout with relatively greater lipid stores compared to departure, others had reduced their relative lipid stores over this first period of independent foraging. While the majority (~74%) of the females increased their lipid contents over the first trip, males were more variable. Smaller seals did better in terms

of their relative growth and increase in energy reserves. This could be explained by a possible bias in return rate acting specifically on smaller seals. Only successful foragers will survive and return, while less successful seals are filtered out early and die at sea. In contrast, despite the higher energy requirements among larger seals, their larger size may still give them an early survival advantage, allowing also less successful seals (in slightly worse condition) to survive and return. This is supported by the generally negative (especially for female pups) relationship between weaning size and probability of return for the midyear haulout. While first-year survival in males increased with total size, lean mass and relative lipid content, these relationships were less clear for female pups. Indeed, after controlling for a weak positive effect of large lean mass, female first-year survival decreased significantly with relative lipid content. This is a radical finding that is not easily explained. We suggest that it may be caused by protein depletion being a more critical factor for survival until seals find food, and that for a given body size, females may utilise relatively more protein for their maintenance than males.

Based on these results, we also develop and discuss a simple model of daily at-sea energy requirements, using data on migration patterns and time budgets obtained from satellite telemetry.

Introduction

The transition to nutritional independence by mammalian offspring is a critical period often associated with significant rates of mortality. In many species this transition is gradual, allowing offspring to develop their food searching and handling skills under guidance from their parents, while still receiving additional nutritional input from their mother's milk. The offspring of these species often have slow growth rates and lactation can last for several months or even years. Among marine mammals, this is the dominant pattern among cetaceans, while pinnipeds show a wide variety of strategies (see Trillmich (1996) for an extensive review). Most otariid (fur seals and sea lions) mothers can be characterised as "income breeders" *sensu* Drent and Daan (1980), making regular trips between breeding beaches where they nurse their pups, and the more or less distant offshore feeding grounds where they must obtain sufficient energy and material to sustain themselves as well as the growing pups. A consequence of this interrupted attendance pattern is comparatively low pup growth rates and long lactation periods (e.g. Trillmich, 1986). The duration of these foraging trips increases as a function of the distance mothers have to travel, and this also has important consequences on pup growth rates (Croxall et al., 1988; Lunn and Boyd, 1993a, b; Trillmich and Limberger, 1985).

Many species of phocid seals are at the opposite extreme of this range of strategies. Land-breeding phocids such as elephant seals (*Mirounga angustirostris* and *M. leonina*) and some populations of the grey seal (*Halichoerus grypus*) are often referred to as "capital breeders" that come ashore for a short and continuous period of lactation and subsequent mating, and during this period they derive all energy for maintenance and milk energy transfer from stored body reserves.

Southern elephant seal pups suckle for ~23 days before their mothers depart (Arnbom et al., 1997; Campagna et al., 1992; Carlini et al., 2000; McCann et al., 1989), and pups remain on the beach fasting for an additional ~ 15 – 65 days (Arnbom et al., 1993; Biuw et al., In Prep.; Carlini et al., 2001). Although it has not been demonstrated, the post-weaning fast on land is believed to play an important role in allowing pups to undergo physiological and behavioural changes preparing them for their critical first feeding trip (Arnbom et al., 1993; Blackwell and Le Boeuf, 1993; Castellini et al., 1994; Thorson and LeBoeuf, 1994), and the timing of departure is likely to reflect a balance between the depletion of body components and the time required for these changes to occur. Because of the long period that elephant seal pups spend in transit before they reach suitable feeding areas, they must leave the breeding beaches while they still have sufficient energy reserves, and the importance of these reserves will vary in response to e.g. variations in prey distribution and abundance.

These different requirements of mothers and offspring suggests that mothers have to balance current energy expenditure to provide sufficient energy to allow her pup a reasonable chance of surviving, while retaining sufficient reserves so as not to compromise her own chance of surviving and/or producing a pup in the following year. The decision by a mother of when to terminate lactation (and fasting) and return to sea is therefore likely to be the result of a complex balance between individual characteristics of the mother (such as age, body size and condition), individual characteristics her pup (for instance body size and composition), and external factors such as environmental fluctuations that may affect prey distribution and abundance across space and time. Previous studies on Southern as well as Northern elephant

seal pups have shown that the rates of protein and lipid utilisation during the post-weaning fast is closely regulated by pups to balance fast duration and energy expenditure against the energy reserves remaining when they depart to sea (Biuw et al., In Prep.; Carlini et al., 2001; Noren et al., 2003). Pups with greater lipid stores at weaning derive almost all (>90%) of their energy from these stores, while leaner pups have to draw on their protein tissue for a considerable fraction (up to 25%) of their energy from protein (Biuw et al., In Prep.; Noren et al., 2003). Fatter pups are able to remain longer on land and burn relatively more lipid, without severely depleting their energy reserves prior to departure, while leaner pups must reduce their lipid catabolism and increase the breakdown of protein, presumably to maintain sufficient lipid to provide some insulation and reserve energy during the transit to feeding grounds. Because energetic yield from every gram of catabolised lipid is more than twice the yield from the catabolism of the same amount of protein, these leaner pups are likely to lose body tissue at higher rates, and may therefore be forced to terminate the land-based fast earlier. The reduced period available for the physiological and behavioural changes may leave these pups less well prepared for life at sea, and this could potentially have negative effects on their initial foraging success compared to their relatively fatter conspecifics.

Biuw et al. (In Prep.) also showed that among leaner pups, males and females differ in the way they allocate their body stores during the post-weaning fast. While lean females tend to spare relatively more lipid at the expense of protein, males tend to maintain a higher energetic contribution of lipid, thereby conserving protein. As a result, while there are no differences in relative lipid content at weaning between

the sexes, females are relatively fatter at departure while males have relatively more lean tissue (Biuw et al., In Prep.). Overall, these adjustments also result in significantly reduced individual variation in lipid content at departure compared to weaning, and females in particular have very similar lipid contents (~40 % lipid) when they go to sea.

Once pups depart from their natal beaches at the end of the fast (late Nov – late Dec), they remain at sea for a period of ~ 6 – 12 months before they again return to land. Pups at sub-Antarctic Macquarie Island travel in a generally south-easterly or south-westerly direction towards and through the polar front (McConnell et al., 2002) and SMRU unpublished data). During this ~ 1000 km transit, lasting for several weeks, pups apparently continue fasting until they have reached suitable foraging grounds (Biuw et al., 2003; McConnell et al., 2002), and the total time spent fasting after weaning may therefore be 2 – 3 months. The period over which pups can survive on stored energy reserves before they must find food will depend on 1) the rate of depletion of the various body stores and 2) the degree to which these stores may be depleted before pups suffer acute effects such as loss of vital lean tissue, such as heart muscle, or critical loss of thermal insulation from blubber. Based on rates of mass loss and estimated changes in body composition during the post-weaning fast, McConnell et al. (2002) estimated that pups are likely to survive for ~ 70 – 80 days on stored reserves. Biuw et al. (In Prep.) used actual measurements of individual mass and body composition changes over the post-weaning fast, and extrapolated these to estimate the time of starvation. Their results suggest that despite the high energetic contribution of lipid which can act to spare their lean tissue while fasting on land,

many pups are approaching critical protein levels at the end of the fast, while they still retain relatively large lipid reserves. Furthermore, assuming that individuals have similar patterns of energy and material use at sea as when fasting on land, pups that derive a high proportion of their energy (~ 15-20%) from the breakdown of protein would be expected to survive a much shorter transit period compared to pups with a high energetic contribution of lipid (Biuw et al., In Prep.).

If individuals survive to reach suitable feeding grounds, their body composition may again affect their ability to hunt and capture prey. For instance, Hindell et al. (1999) and Irvine et al. (2000) showed that larger elephant seal pups can dive for longer periods compared to smaller pups, and variations in buoyancy related to body composition (Beck et al., 2000; Biuw et al., 2003; Webb et al., 1998) may have important consequences on the energy expenditure while diving. Variations in early foraging success may also affect migration and haulout patterns. While some individuals return for a so-called “midyear haulout” (around May – July), lasting for ~ 10 – 25 days (Wheatley, 2001), others are not seen again until the first moult (~ December). Among female pups, there is a negative relationship between weaning body mass and the probability of a seal returning for the midyear haulout, while no such relationship has been found for males (Wheatley, 2001). These patterns may reflect sex differences in either early foraging success related to body composition, or they may simply reflect differences in behaviour patterns between males and females. Although the effects of individual variation in energy expenditure and partitioning of body stores during the post-weaning fast have been extensively researched, no studies

to date have linked these variations to the early survival and changes in body condition during the initial period of independent feeding.

In this paper, we build on previous studies of maternal expenditure and fasting energetics of newly weaned pups by describing the changes in body mass and composition of Southern elephant seal pups from Macquarie Island during their first year after reaching nutritional independence. We will also briefly describe the apparent links between body condition and the probability of individuals returning for the midyear haulout and the first moult, and examine in some detail how the probability of seals surviving their first year is affected by size and body composition at weaning. We will also discuss the possible mechanisms behind the observed net changes in body composition and energy content in terms of the day-to-day changes while at sea. To do this, we make general references to data on migration patterns and foraging behaviour from a sub-sample of the individuals included in our study, obtained through satellite telemetry. The aim here was to develop a simple model of energy expenditure and estimated gross energy intake of elephant seal pups while foraging at sea.

Materials and Methods

Study site and field procedures

This study was carried out at Macquarie Island in the Southwest Pacific sector of the Southern Ocean (54° 30'S, 158°57'E, Figure 0) in 1998 and 1999. We selected our sample from a larger population of individually marked, recently weaned southern

elephant seal pups from the Isthmus breeding colony, which were weighed and measured at birth and weaning as part of a large-scale mark/recapture program carried out between 1993 and 2001 (McMahon et al., 2000b, 2003).

Seals were captured and weighed according to (McMahon et al., 2000a). The axial girth was measured just behind the base of the front flippers, and the standard nose-to-tail length was measured as the straight line between the tip of the nose to the tip of the tail. We used isotopically labelled water (e.g. (Nagy and Costa, 1980; Reilly and Fedak, 1990)) to measure the body composition of pups at weaning, prior to departure. Immediately after capture, a blood sample was collected from the extradural vein to measure the background isotope level. A weighed dose of either 4 - 8 ml of deuterium oxide (HDO, specific concentration: 99.9%) or approximately 2 mCi tritiated water (^3HHO) in 4 ml of distilled water was then injected using either a 10 ml or 5 ml plastic syringe. The syringe was flushed with blood three times to ensure complete delivery of the labelled water. A second blood sample was taken 2-3 hours after initial injection for determination of dilution space and calculation of body composition. Blood samples were centrifuged and the plasma transferred to 2 ml cryo tubes and these were stored at -20°C until further analysis. Samples for deuterium analysis were transferred to 100 μL capillary glass pipettes, that were flame sealed and stored frozen at -20°C until further analysis.

Re-sight effort and protocol

The permanent research station at Macquarie Island provided an ideal year-round base, and we were able to maintain a high re-sighting effort over the entire three

years of the study. The main Isthmus breeding beaches were re-sighted daily throughout the year, while the top 3rd of the island was covered once every week, and monthly re-sighting trips were conducted to cover the remaining potential haulout sites around the entire coastline. Moreover, *ad hoc* re-sights were also reported by other personnel travelling in the field, in particular the parks rangers. When seals were encountered or reported, we captured and handled them according to the methods previously described. Seals returning to the Isthmus were usually captured on the day they were first seen, while seals encountered or reported elsewhere on the island were captured as soon as possible (usually within 3-4 days after the first sighting).

Laboratory procedures

Tritiated samples

We analysed plasma samples for ^3H specific activity by liquid scintillation counting. Weighed plasma samples of approximately 100 μl were added to 10 ml of PicoFlour scintillation cocktail (Packard Instruments) and counted in triplicate for 10 minutes on a Packard Tri-Carb® 2000 liquid scintillation counter. Correction for quenching was made by automatic external standardization. We prepared standard dilutions by gravimetric dilution of an aliquot of the injectate to the approximate dilution expected in the seals, and these were also counted in triplicate for 10 min. The exact water content of each plasma sample was determined by transferring ~100 μl of the sample to a weighed glass slide. The slide was weighed again and then dried on a hot plate at a temperature of ~ 50°C until complete evaporation of the plasma water, and the slide was then weighed a third time. In this way we could correct the specific activity of ^3H for the exact plasma water content.

Deuterated samples

Blood samples were distilled using the pipette method of Nagy (1983). Mass spectrometric analysis of deuterium enrichment was performed using H₂ gas, produced from the distilled water after reaction with LiAlH₄ (Ward et al 2000). ²H: ¹H ratios were measured using dual inlet gas source isotope ratio mass spectrometry (Optima, Micromass IRMS), with isotopically characterised gases of H₂ (CP grade gases BOC Ltd) in the reference channel. Reference gases were characterised every 3 months relative to SMOW and SLAP supplied by IAEA. Each batch of samples was run with triplicates of three laboratory standards to correct for day-to-day variation in performance of the mass spectrometers. All isotope enrichments were measured in delta (per mil) relative to the working standards and converted to ppm, using the established ratios for these reference materials. Measures of isotope enrichment were based on independent analysis of two sub-samples of the water distilled from the blood samples, which were analysed blind to their biological source.

Isotope dilution calculations

We calculated total body water (TBW) according to the empirically derived equation for grey seals (Reilly and Fedak, 1990) as:

$$TBW = 0.382 + 0.965(HDOspace) \quad \text{Equation 1b}$$

or:

$$TBW = -0.234 + 0.971(^3HHOspace) \quad \text{Equation 1a}$$

The proportion of lipid (*%TBL*) and protein (*%TBP*) and the total body gross energy (*TBGE*) were calculated according to the same authors as:

$$\%TBL = 105.1 - 1.47(\%TBW) \quad \text{Equation 2}$$

$$\%TBP = 0.42(\%TBW) - 4.75 \quad \text{Equation 3}$$

$$TBA = 0.1 - 0.008(BM) + 0.05(TBW) \quad \text{Equation 4}$$

$$TBGE = 40.8(BM) - 48.5(TBW) - 0.4 \quad \text{Equation 5}$$

where *%TBW* is calculated from *BM* is body mass in kg, and *%TBW* is calculated from body mass and *TBW*, and energy is expressed in MJ. Calculations of *TBGE* assumed energy densities of 39.5 and 23.5 kJ/g for lipid and protein respectively (Reilly and Fedak, 1990).

Numerical and statistical analyses

We used the R package (Ihaka and Gentleman, 1996) for all data analyses. All summary statistics of central tendency are reported as mean \pm 1 standard deviation unless otherwise stated.

Standard diagnostic tests and conversions

For simple comparisons between samples (i.e. years, sexes or captures) we used classical parametric and non-parametric methods (included in the `ctest` library for R). In order to determine whether variables were normally distributed we used Shapiro-Wilks test for normality. We tested for homogeneity of variances between

two normally distributed samples using a standard variance ratio F-test, while for non-normally distributed samples we used the Ansari-Bradley two-sample test for a difference in scale parameters. We then tested for differences in central location (e.g. mean or median) between two samples using either a standard two-sample t-test (equal or unequal variances) for normally distributed variables, or the two-sample Wilcoxon rank sum test in the case of non-normal samples. In the results section, we refer to a t-test with equal or unequal variances as: $t\text{-test}_E$ and $t\text{-test}_U$ respectively.

Statistical models of functional relationships

We used a combination of Linear Models, Generalized Linear Models (GLM) and Quantile Regression to examine functional relationships between variables. Linear models were used in cases where we could assume that the errors around the mean response were normally distributed, and this was the assumed method unless otherwise stated in the text. In cases where the assumption of normality was likely to be violated, we fitted GLMs with appropriate specifications of the link and variance functions. For instance, if the response was assumed to be linearly related to the explanatory variable(s) but the variance appeared to increase as a function of the mean response, we used a quasi family (denoted as GLM_{Quasi} in the text) with an identity link and a variance function (θ) that was related to the mean response (μ) according to: $\theta = \mu^2$. In situations when error distributions were not easily determined, we used quantile regression as a non-parametric alternative e.g. (Koenker and Bassett, 1978). In quantile regression, a model is fitted by minimising the sum of absolute residuals, conditional on a pre-specified quantile value of the dependent variable (i.e. 0.5 for the

median). Quantile regressions were also used for describing edges in two-dimensional scatter plots.

We used Analysis of Deviance (ANODEV) to test for significance of GLM model parameters (McCullagh and Nelder, 1983). GLM models were compared using the Akaike Information Criterion (AIC , (Akaike, 1973)), and model selection was based on Akaike weights (Burnham and Anderson, 1998). These weights are calculated as:

$$AIC_w = \frac{\exp(-\frac{1}{2}dAIC)}{\sum_{r=1}^R \exp(-\frac{1}{2}dAIC_r)}$$

where $dAIC$ is the difference in AIC between each model and the “best” in the set of candidate models. These weights therefore provide a normalised index of the likelihoods of each model in the set.

Re-sight and survival models

We did a series of analyses to test whether body size (mass) had any influence on the probability of an animal being seen during 1) the midyear haulout and 2) the first moult. These analyses were carried out using logistic GLMs, and were based on two different datasets. The first set (Set 1) contained all seals that had previously been marked and weighed at weaning in the years 1998 – 2000. In the second set (Set 2), only those individuals from the first set that were subsequently seen at least once *after the end* of the first moult were analysed. Therefore, the analyses of the first set

does not control for mortality occurring during the first year, and will lead to an underestimate of the probability of resight. In contrast, the second set of analyses attempts to control for first-year mortality by analysing only confirmed survivors. This method may still lead to slightly biased estimates, because of the probability of a seal not being seen upon return to the island. However, we expect this bias to be independent on the covariate analysed (i.e. body mass in this case), because of the very extensive and continuous re-sighting effort. Although there are methods available for estimating recapture probability, and to correct the survival estimates accordingly (Lebreton et al., 1993), there is some uncertainty as to the accuracy of the handling of covariates in currently available packages (for instance Program MARK, (White and Burnham, 1999)).

In a similar way as these analyses, we also tested the effects on early body composition on the probability of seals surviving their first year. The seals for these analyses were selected from the sample of pups for which we measured body composition at weaning using the isotope dilution methods. The criteria here were otherwise the same as for Set 2 above, i.e. seals had to be seen at least once after the end of the first moult.

Results

General overview of changes over the first year

In this section we provide a general overview of the changes in mass and body composition that were observed over the first year (see Figure 1). In subsequent

sections we analyse each period in more depth. Details of the changes occurring over the post-weaning fast have been described previously in Biuw et al. (In Prep.), and these measurements are also shown in Figure 1 to provide a more complete picture of the development of pups over the first year of life. The data on subsequent captures were collected from many of the same individuals as in the earlier paper. However, some individuals that were measured at weaning (WC) and at pre-departure (PD) were not seen or recaptured subsequently during the first year. Furthermore, we also captured a number of additional seals at departure to compensate for known individuals that left the beaches before they could be recaptured. Although the mass at weaning was known for these additional seals, the body composition was not known.

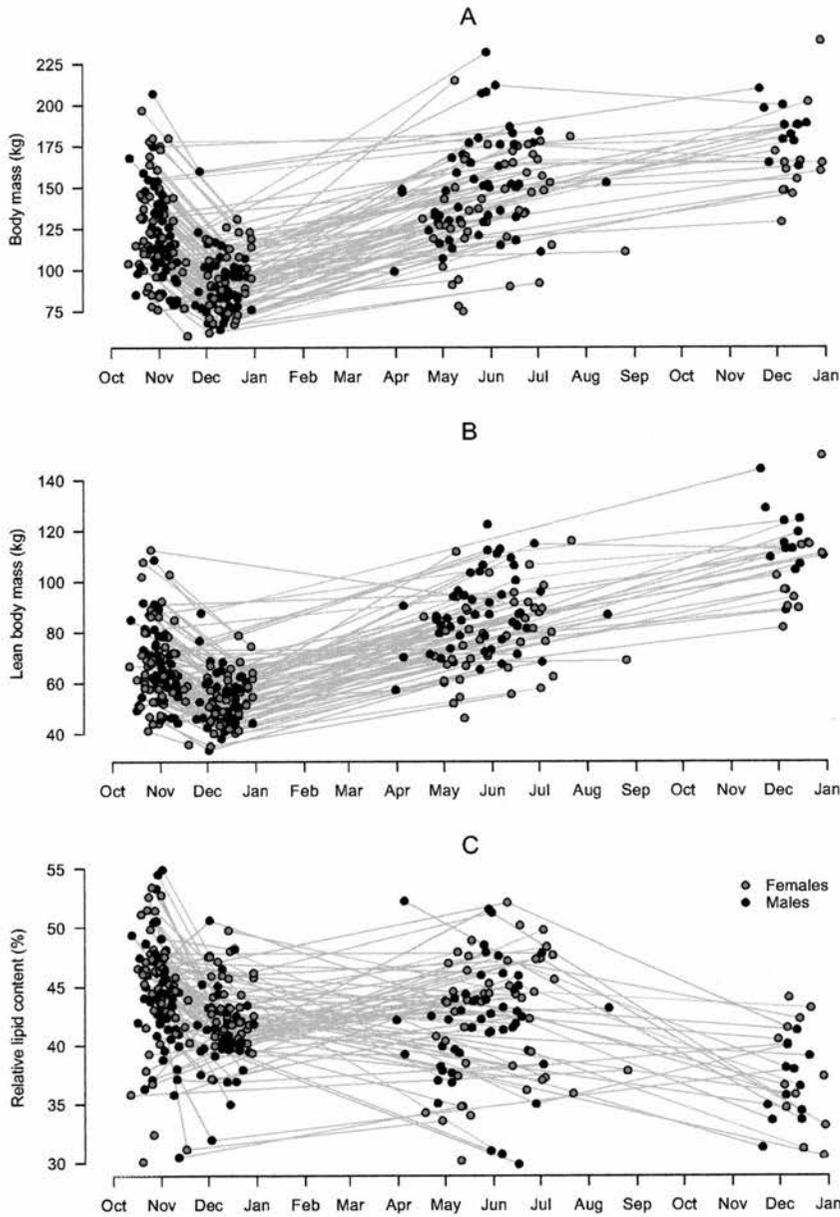


Figure 1. Overview of changes in A) total body mass, B) lean mass (i.e. lipid-free mass), and C) relative lipid content over the first year. Data are presented for all seals measured on at least two occasions. The four measurement times are (from left to right): 1. beginning of post-weaning fast (“weaning”), 2. end of post-weaning fast (“departure”), 3. return for the midyear haulout (“midyear”), and 4. return for the first moult (“moult”). Measurements at the end of the midyear haulout are not presented.

There was considerable variation in the timing and number of times individual seals returned to land during the first year. While some individuals returned for the midyear haulout (MYR) between late March and late August (May 29 ± 27.0 days) and again at the first moult between late November and early January (Dec 10 ± 10.4 days), others were not seen during the midyear but returned for the first time at the first moult. The mean age of seals returning at midyear was 240.9 ± 27.2 days (~8 months), while the mean age of seals returning at the moult was 433 ± 12.1 days (~14 months). Body mass (*BM*) and composition changed dramatically between the various haulouts, and there were considerable individual variations in these changes. In general, *BM* increased from the first departure until they returned to Macquarie either at midyear or moult. The increase appeared to be slightly greater between first departure and midyear than between midyear and moult. However, this is due in part to the fact that seals were not recaptured at the end of the midyear haulout fast, so the changes shown in Figure 1 are from midyear return to moult return. In contrast to the pattern for overall *BM*, the rate of increase in lean body mass (*LBM*) appeared to be similar between midyear and moult as between first departure and midyear (Figure 1B). The changes in relative lipid content (*%TBF*) followed a very different and less consistent pattern (Figure 1C). While some individuals increased their *%TBF* between first departure and midyear return, others showed a decrease. In contrast, there was a clear negative trend in *%TBF* between the start of the midyear haulout and the start of the first moult. In the following sections we present detailed analyses for each of these time segments.

Departure to midyear haulout

Summary statistics on body mass, condition and energy content before departure and at the return for the midyear haulout are presented in Table 1, along with derived measures of changes occurring over this first period. We first present summary and group statistics for the point measurements at departure and return. It is important to emphasise that these figures are unlikely to be representative of the entire population, since our study was designed to provide a uniform selection of individuals throughout the entire size range, (see Biuw et al. (In Prep.) for further discussion).

Departure

Body mass at departure ranged from 62 – 126 kg (88.2 ± 16.9 kg) and there were no sex differences ($t_{40.5} = -0.169$, $p = 0.866$) or differences between years ($t_{47.6} = 1.254$, $p = 0.216$). Lipid comprised 30.5 – 50.6 % (41.7 ± 3.8 %) or equivalent to 24.0 to 62.7 kg (37.0 ± 8.8 kg), while protein comprised 10.8 – 16.6 % (13.4 ± 1.1 %), or 7.3 – 17.9 kg (11.7 ± 2.1 kg), and water 37.1 – 50.8 % (43.2 ± 2.6) or 25.2 – 56.5 kg (38.0 ± 6.9 kg) of total body mass. Total body lipid (*TBF*) was not significantly different between males and females (t-test_E: $t_{49} = 0.448$, $p = 0.656$) or between years (t-test_E: $t_{49} = 1.345$, $p = 0.185$). Similarly, there was no difference in %*TBF* between females and males (Wilcoxon rank sum test: $W = 387$, $p = 0.173$), or between years (t-test_U: $t_{32.1} = 0.851$, $p = 0.401$). The total protein content (*TBP*) was not significantly different between the sexes (t-test_E: $t_{49} = -0.873$, $p = 0.387$), or years (t-test_E: $t_{49} = 0.916$, $p = 0.364$). There was a more than twofold difference in total body energy content (*TBGE*) at departure, ranging from 1244 – 2849 MJ (1759 ± 390.3 MJ). The distribution over this range was significantly different from normal (Shapiro-

Wilks test of normality: All seals: $W = 0.938, p = 0.0106$, Females: $W = 0.908, p = 0.0498$, Males: $W = 0.940, p = 0.094$). While the mean energy content did not differ between males and females (Wilcoxon rank sum test, $W = 309, p = 0.917$), the variance was significantly higher for females than males (variance ratio = 1.87, Ansari-Bradley test: $AB = 226, p = 0.047$).

Return

At the midyear haulout, *BM* ranged from 90 – 232 kg (145.7 ± 29.6 kg), and did not differ significantly between the sexes ($t_{45.7} = -0.503, p = 0.618$) or between years ($t_{46.1} = 0.218, p = 0.829$). Lipid comprised 29.9 – 52.1 % (42.3 ± 4.8 %), or 34.1 – 119.6 kg (62.3 ± 17.5 kg), while protein comprised 10.4 – 16.7 % (13.2 ± 1.4 %), or 12.9 – 27.0 kg (19.0 ± 3.3 kg), and water 36.0 – 51.2 % (42.7 ± 3.2 %), or 40.9 – 84.5 kg (61.8 ± 10.8 kg). Females had slightly but significantly higher %*TBF* compared to males (mean: 43.7 and 41.3 % respectively, Wilcoxon rank sum test: $W = 423, p = 0.020$), and the relative protein content (%*TBP*) was consequently higher for males (Wilcoxon rank sum test: $W = 207, p = 0.040$). There were no differences between years in either of these proportions (Wilcoxon rank sum test: $W = 207, p = 0.98$). The range of *TBGE* of returning pups was more than threefold, from 1687 – 5367 MJ (2947 ± 751.4 MJ), and the distribution was not significantly different from normal in females (Shapiro-Wilks test of normality: $W = 0.973, p = 0.800$), was significantly so in males (Shapiro-Wilks test: $W = 0.900, p = 0.008$). The mean *TBGE* was not significantly different between males and females (Wilcoxon rank sum test: $W = 347, p = 0.547$), and despite the difference in distribution between males and females, the

variance was not significantly different (Ansari-Bradley test: $AB = 294$, $p = 0.549$).

	1998				1999			
	Females (n=9)		Males (n=16)		Females (n=12)		Males (n=14)	
DEPARTURE	Mean:	SD:	Mean:	SD:	Mean:	SD:	Mean:	SD:
Age (days)	59.44	13.20	53.69	8.13	72.09	5.47	72.36	9.39
Fast duration (days)	35.78	11.30	29.56	7.14	47.00	6.06	47.21	8.49
Body mass (kg)	93.11	20.78	90.25	16.83	83.75	15.42	86.71	16.39
Body length (cm)	137.00	10.90	136.38	8.72	128.08	9.35	132.43	10.64
Axial girth (cm)	123.56	9.88	120.86	8.93	118.75	11.58	119.93	7.07
Total body water (kg)	38.68	6.33	39.14	8.34	36.00	5.86	37.82	6.64
Total body lipid (kg)	40.99	13.37	37.32	7.34	35.10	7.97	35.54	7.67
Total body protein (kg)	11.82	1.75	12.15	2.76	11.14	1.75	11.77	2.02
% body water	42.12	3.80	43.24	3.22	43.15	1.65	43.74	1.23
% body lipid	43.19	5.58	41.53	4.74	41.67	2.43	40.81	1.81
% body protein	12.94	1.59	13.41	1.35	13.37	0.69	13.62	0.52
Total body energy (MJ)	1922.37	565.94	1783.66	332.98	1670.52	355.70	1703.07	352.22
RETURN								
Age (days)	249.44	25.79	233.75	21.41	246.73	23.59	245.43	29.57
Days after weaning	225.78	25.24	209.63	22.13	221.50	23.52	220.29	29.89
Mass (kg)	143.11	25.67	148.63	37.10	143.33	30.91	146.07	23.54
Body length (cm)	157.89	9.77	158.54	13.32	156.25	14.17	160.93	8.92
Axial girth (cm)	137.78	11.99	138.54	13.38	136.00	10.43	134.71	7.81
% body water	42.90	3.40	44.11	3.53	40.85	2.43	42.65	2.92
% body lipid	42.04	5.00	40.26	5.19	45.04	3.57	42.41	4.29
% body protein	13.27	1.43	13.78	1.48	12.41	1.02	13.16	1.23
Total body water (kg)	61.04	10.13	64.76	12.62	58.04	10.30	62.11	9.59
Total body lipid (kg)	60.68	14.86	61.00	22.56	65.32	17.99	62.23	13.20
Total body protein (kg)	18.84	3.19	20.14	3.70	17.57	2.91	19.15	3.04
Total body energy (MJ)	2878.17	636.35	2922.41	964.27	3032.59	780.65	2947.17	568.64
CHANGES								
Trip duration (days)	190.00	19.00	180.06	22.90	174.50	20.17	173.07	27.47
Total mass change (kg)	50.00	11.17	58.38	24.79	59.58	22.02	59.36	13.97
Net water change (kg)	22.35	4.46	25.63	6.77	22.04	7.72	24.28	6.85
Net lipid change (kg)	19.69	9.86	23.68	20.18	30.22	12.72	26.69	8.53
Net protein change (kg)	7.01	1.64	7.99	2.16	6.43	2.26	7.38	2.36
Net water change (%)	0.78	3.35	0.87	5.05	-2.29	2.00	-1.09	2.67
Net lipid change (%)	-1.15	4.93	-1.27	7.42	3.37	2.94	1.60	3.92
Net protein change (%)	0.33	1.41	0.36	2.12	-0.96	0.84	-0.46	1.12
Net energy change (MJ)	955.80	384.03	1138.75	809.90	1362.08	551.07	1244.10	349.92
Daily lipid gain (kg)	0.10	0.05	0.13	0.10	0.18	0.09	0.16	0.06
Daily protein gain (kg)	0.04	0.01	0.04	0.01	0.04	0.02	0.04	0.02
Daily net energy gain (MJ)	5.08	2.07	6.32	4.19	8.03	3.83	7.44	2.61
Energy from lipid (MJ)	777.70	389.53	935.33	796.94	1193.84	502.51	1054.26	336.87
Energy from protein (MJ)	164.83	38.65	187.79	50.80	151.02	53.13	173.40	55.41
Relative lipid energy (%)	77.12	14.82	61.43	66.98	86.53	5.22	83.87	7.07
Relative protein energy (%)	21.41	14.53	36.79	65.65	12.18	5.11	14.79	6.93

Table 1. Summary statistics based on individual measurements at the end of the post-weaning fast ("DEPARTURE") and return for the midyear haulout ("RETURN"), and derived measures of change over this period. Relative lipid and protein energy are calculated using energy densities of 39.5 and 23.5 kJ/g for lipid and protein respectively (Reilly and Fedak, 1990). Positive values indicate an increase while negative values represent a decrease. Changes in relative proportions are expressed in units of percent, for instance a change in lipid content from 40 to 30 % represents a decrease by 10 percent units.

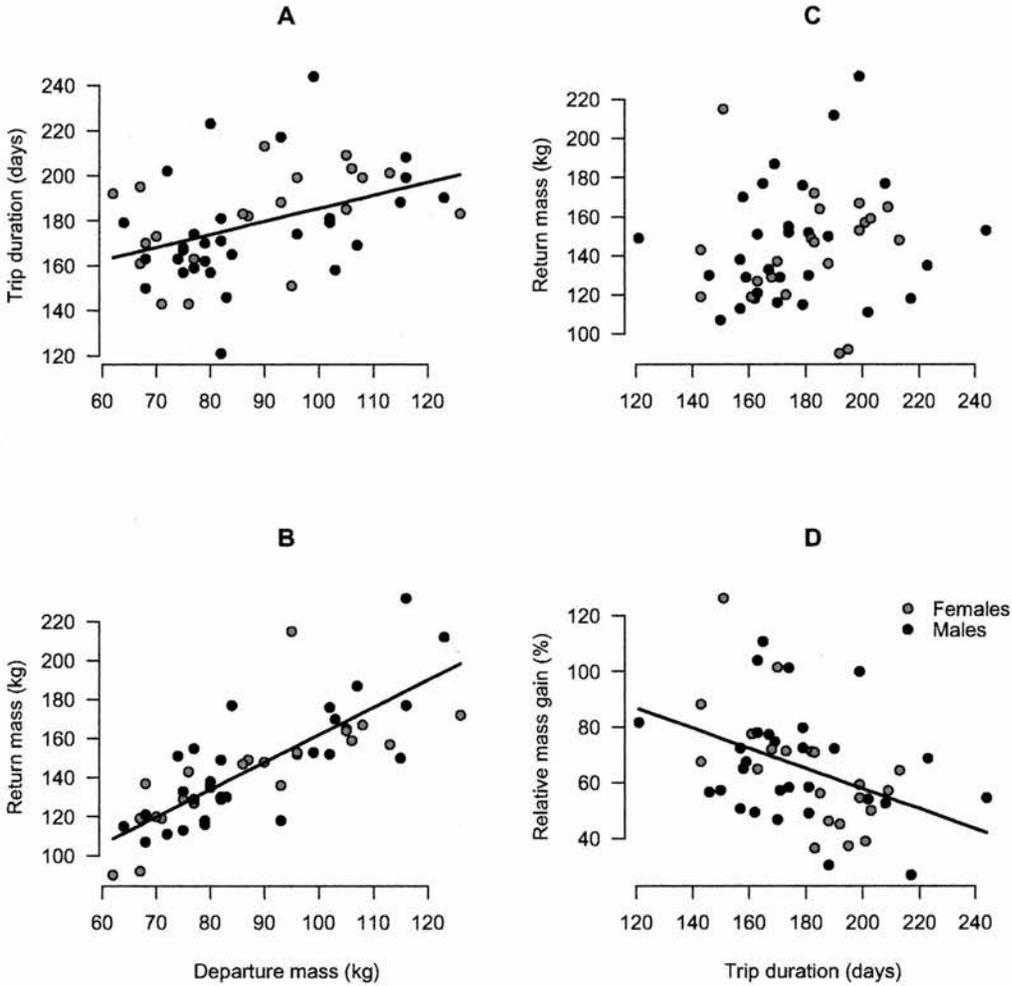


Figure 2. Bivariate scatter plots of relationships between body mass at the end of the post-weaning fast (“departure”) and midyear return, and trip duration. Departure mass is the independent (x) variable in Figs. A and B, while trip duration is the independent variable in Figs. C and D. Relative mass gain is the change in mass over the trip divided by departure mass, and is expressed in percent. See text for regression statistics and diagnostics.

Changes and functional relationships over the first trip

The duration of the first trip increased with departure mass ($DUR_{Tr} = 128.0 + 0.57(BM_D)$, $F_{1,48} = 10.07$, $r^2 = 0.16$, $p = 0.003$, where DUR_{Tr} denotes trip duration and BM_D denotes body mass at departure Figure 2A). Body mass at return also

increased with departure mass (GLM_{Quasi}: $BM_R = 21.6 + 1.4(BM_D)$, *Deviance Residual* = 1.23, $p < 0.0001$, Figure 2B). Neither of these relationships varied between the sexes (ANCOVA: $t = -0.78$, $p = 0.44$ and ANODEV: *Deviance residual* = 0.001, $p = 0.75$) or between years (ANCOVA: $t = -1.12$, $p = 0.27$ and ANODEV: *Deviance residual* = 0.035, $p = 0.13$). There was no relationship between trip duration and return mass in a bivariate analysis ($F_{1,48} = 0.9746$, $r^2 = 0.02$, $p = 0.328$, Figure 2C). However, when return mass was modelled as a function of both BM_D and DUR_{Tr} , there was a significant negative relationship between trip duration and return mass, conditional on the positive relationship between mass at departure and return (GLM_{Quasi}: $BM_R = 58.3 + 1.55(BM_D) - 0.28(DUR_{Tr})$, *Deviance Residual* = 0.091, $p = 0.009$, where the deviance residual and p values refer to the effect of including trip duration in addition to departure mass, see also Table 2 A).

Response	Model	Parameter estimate (Mean SE)	Deviance	Residual Df	Residual Deviance	p (χ^2)
A.						
Return mass (kg)	Null model	58.26 ± 19.00		49	1.940	
	Departure mass	1.56 ± 0.16	1.238	48	0.701	< 0.0001
	Trip duration	-0.28 ± 0.11	0.091	47	0.610	0.009
B.						
Relative mass gain (%)	Null model	129.87 ± 21.59		49	4.866	
	Departure mass	-0.12 ± 0.17	0.309	48	4.557	0.060
	Trip duration	-0.30 ± 0.12	0.526	47	4.032	0.014

Table 2. ANOVA tables presenting comparisons of General Linearized Models (GLMs) of return mass (A) and relative mass gain (B) of southern elephant seal pups from the end of the post-weaning fast until the return to the first midyear haulout at Macquarie Island. The GLM was fitted using a quasi family that allows the specification of the variance function. To account for the non-uniform variance distribution, we assumed that this variance function (θ) was related to the mean (μ) of the response variable according to: $\theta = \mu^2$.

The net mass gained over the trip ranged from 25 – 120 kg (57.4 ± 19.3 kg), representing a relative mass gain of 26.8 – 126.3 % (65.7 ± 20.7). Measured in kilograms, this gain increased with departure mass (GLM_{Quasi}: $GAIN_{Net} = 23.0 + 0.39(BM_D)$, *Deviance residual* = 0.58, $p = 0.015$, where $GAIN_{Net}$ denotes the net mass gain), and this relationship did not vary with sex or year (ANODEV: *Residual deviance* = 0.012, $p = 0.739$ for gender effect and *Residual deviance* = 0.207, $p = 0.147$ for year effect). The slope was significantly less than 1 ($t = -3.89$, $p = 0.0003$), and consequently the relative mass gain decreased significantly with trip duration (GLM_{Quasi}: $GAIN_{Rel} = 124.7 - 0.33(DUR_{Tr})$, *Deviance residual* = 0.79, $p = 0.002$). When relative mass gain was modelled as a function of both departure mass and trip duration, only the latter contributed significantly to the model fit (GLM_{Quasi}: $GAIN_{Rel} = 129.9 - 1.12(BM_D) - 0.30(DUR_{Tr})$, *Deviance Residual* = 0.091, $p = 0.009$, Table 2 B).

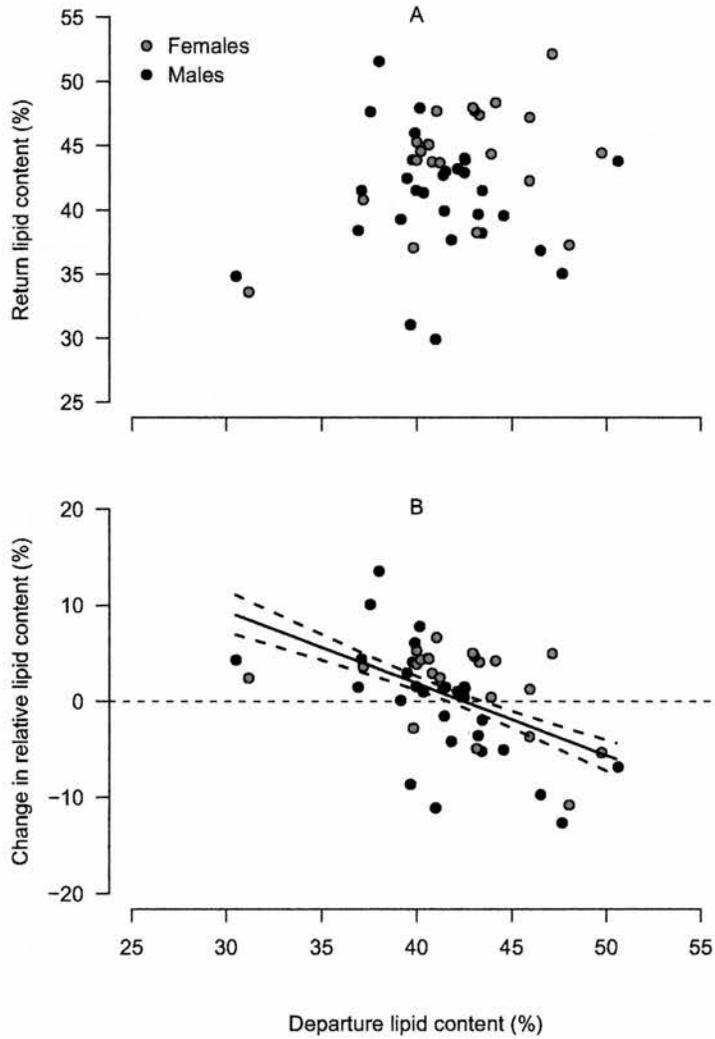


Figure 3. Relationship between relative lipid content at departure and A) relative lipid content at midyear return and B) the change in relative lipid content. This change is expressed as percent units, i.e. a change from a lipid content of 40 % to 35 % is a change of 5 percent units.

The net change in total body lipid (*TBF*) over the first trip ranged from a decrease of 2.8 kg to an increase of 75.5 kg (25.1 ± 14.3 kg), and when the only individual that decreased its lipid content was excluded, the increase for the remaining seals represented 9.6 – 65.1 % (42.6 ± 12.5 %) of the total mass gain. The increase in total body protein (*TBP*) ranged from 2.9 – 13.9 kg (7.3 ± 2.2 kg), and represented 6.7 –

28.5 % (13.4 ± 4.12 %) of the total mass gain, while total body water (*TBW*) increased by 10.7 – 43.4 kg (23.7 ± 6.7 kg), representing 27.2 – 79.2 % (43.2 ± 9.9 %) of the total mass change. On average, there was a direct proportional relationship between *TBF* at departure and at return (GLM_{Quasi}: $TBF_R = 14.9 + 1.28(TBF_D)$, *Deviance residual* = 1.423, $p < 0.0001$). Since the slope was not significantly different from 1 ($t = 1.18$, $p = 0.24$) the change in *TBF* over the trip was not related to *TBF* at departure (GLM_{Quasi}: *Deviance residual* = 0.184, $p = 0.42$). Furthermore, while there was no relationship between relative lipid content (%*TBF*) at departure and return ($F_{1,49} = 1.90$, $p = 0.175$, Figure 3A), the change in %*TBF* over the trip (expressed as percent units) decreased with %*TBF* at departure ($\Delta\%TBF = 32.1 - 0.76(\%TBF_D)$, $F_{1,48} = 18.54$, $r^2 = 0.26$, $p < 0.0001$, Figure 3B). There was no difference in slopes between males and females (ANCOVA: $t_{2,47} = -1.78$, $p = 0.079$). However, of the 21 females in our sample, sixteen had a positive $\Delta\%TBF$ while the remaining five showed a net decrease (ratio = 3.2). This ratio was significantly different from 1 (Monte Carlo $\chi^2_{10000} = 5.76$, $p = 0.016$). Among males, 19 seals increased and 11 decreased their %*TBF* (ratio = 1.7), and this ratio was not significantly different from 1 (Monte Carlo $\chi^2_{10000} = 2.13$, $p = 0.144$).

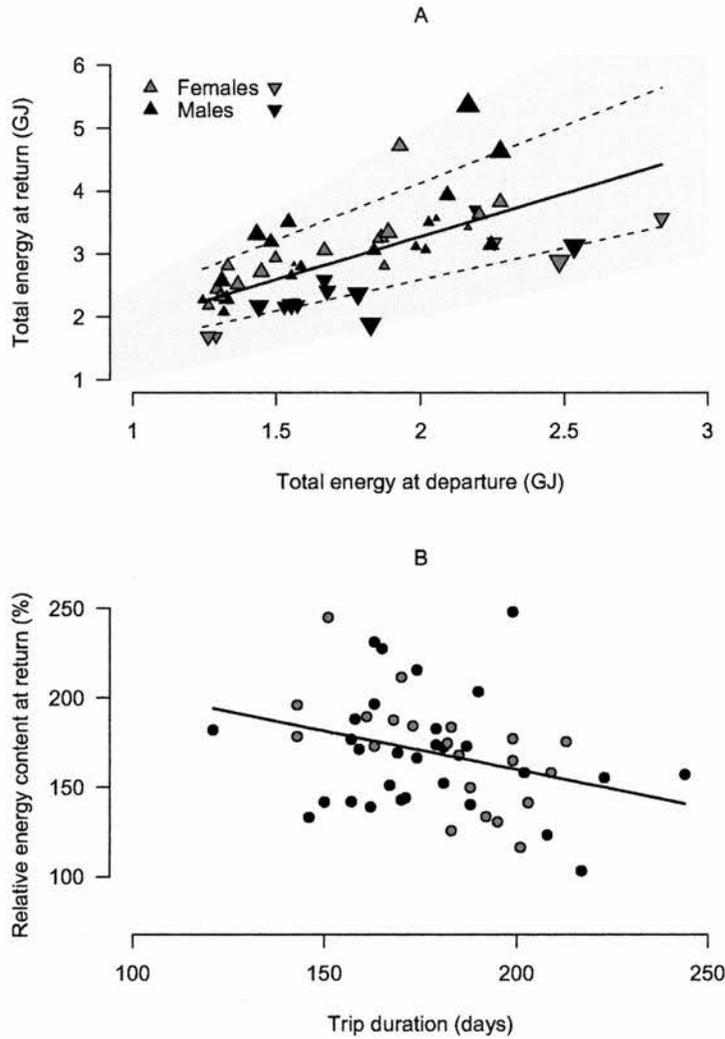


Figure 4. Relationships between energy content at departure, trip duration, and energy content at the midyear return. The lower boundary of the grey shaded area in A represents the 1:1 relationship (i.e. zero change) in energy content over the trip, while the upper boundary represents An energy content at return of 2.5 times the energy content at departure (i.e. an increase of 150%). The solid line represents a fitted GLM, while the broken lines represent the 10 and 90% conditional regression quantiles through the data. Triangles indicate the direction of change relative lipid content (point up = increase, point down = decrease), while their sizes indicate the relative magnitude of the change.

All seals that returned at midyear increased their energy content over the trip (mean increase = 1188 ± 581.1 MJ), but the magnitude of this increase differed considerably between individuals, from 60 to 3202 MJ. This represents a relative increase of between 3.3 and 147.9 % (69.2 ± 31.6 %). The absolute energy content at return increased with energy content at departure (GLM_{Quasi}: $TBGE_R = 552.5 + 1.36(TBGE_D)$, *Deviance residual* = 1.145, $p < 0.0001$, Figure 4A). However, as shown in Figure 4A, the variation around this overall relationship was not uniform, but increased with increasing initial energy content. We therefore modelled the lower and upper “edges” of these data using the 10 % and 90 % quantile regressions. The 10 % quantile model for the lower edge had the following form: $TBGE_R^{Q10} = 591.9 + 1.00(TBGE_D)$, $t_{1,49} = 2.56$, $p = 0.014$. This slope coefficient was not significantly different from 1 ($t_{1,49} = 0.0022$, $p = 0.998$), and seals around this lower boundary therefore increased their energy content by an almost constant amount represented approximately by the intercept (591.9 MJ). The 90% quantile model were of the form: $TBGE_R^{Q90} = 531.5 + 2.51(TBGE_D)$, $t_{1,49} = 4.06$, $p = 0.0002$. This slope coefficient (2.51) was significantly different from 1 ($t_{1,49} = 2.44$, $p = 0.018$), and seals along this upper edge therefore increased their energy content by a factor of ~2.5. The values for net energy gains translated into net daily energy gains ranging from 0.28 – 18.5 MJ/day (6.8 ± 3.5 MJ/day). There was no relationship between initial energy content and the daily net rate of energy gain ($F_{1,49} = 0.145$ $p = 0.705$). However, the relative energy gain (%EG; return energy content as a proportion of departure energy content) decreased significantly with increasing trip duration ($\%EG = 246.2 - 0.43(DUR)$, $F_{1,49}: 5.45$, $r^2 = 0.1$, $p = 0.024$), although the unexplained variation around this regression line was substantial (Figure 4B).

Midyear to moult

All moult captures

Only 25 animals were captured at the return for the first moult (12 females and 13 males), and summary statistics for these seals are presented in Table 3A, and will only briefly be presented here. Males were on average ~ 15 kg heavier ($p = 0.0359$), a difference mainly caused by significantly higher total body water (and therefore lean tissue) in males compared to females ($p = 0.0442$). While there was no significant difference in total lipid content ($p = 0.2109$), and only a weak tendency for males to have greater amounts of total protein (0.0502), the lean tissue (i.e. lipid-free mass) was about 12 kg greater in males ($p = 0.0339$).

Changes between midyear and moult

Among the seals that were captured and measured at the moult return, only 14 had previously been captured and measured at the return for the midyear haulout (see Table 3B for summary statistics). Ten seals (6 males and 4 females) increased their mass over this period, while three seals (2 females and one male) decreased their mass and one seal (male) had the same mass at both returns. The period between the midyear and moult returns decreased with increasing midyear mass (Median regression: $DUR_{MM} = 263.54 - 0.51(BM_{MYR})$, $t_{1,12} = -2.342$, $p = 0.0373$, where DUR_{MM} denotes the number of days between returns and BM_{MYR} denotes body mass at the midyear return, Figure 5A). This was a result of the positive relationship between body mass at the first departure and the duration of the first trip (Figure 1A and 2A), while the timing of the moult return was not related in a consistent way to midyear mass (Median regression, $t_{1,12} = -0.9425$, $p = 0.3645$).

A. MOULT RETURN	Females (n=12)		Males (n=13)		Kruskal-Wallis		
	Mean:	SD:	Mean:	SD:	X ²	p	
Age (days)	435.92	14.43	430.00	8.96	0.656	0.4180	
Days since weaning	411.33	14.57	404.92	11.26	0.758	0.3839	
Body mass (kg)	167.33	28.47	182.77	16.69	4.401	0.0359	*
Body length (cm)	168.50	11.16	174.38	8.71	2.852	0.0913	.
Axial girth (cm)	142.00	7.93	147.00	5.80	4.091	0.0431	*
Total body water (kg)	76.70	13.06	85.17	9.62	4.050	0.0442	*
Total body lipid (kg)	63.12	14.50	66.88	6.99	1.565	0.2109	
Total body protein (kg)	24.27	4.28	27.09	3.32	3.834	0.0502	.
Lean body mass (kg)	104.20	17.88	115.90	13.35	4.500	0.0339	*
% body water	45.93	3.18	46.55	2.06	0.358	0.5496	
% body lipid	37.58	4.68	36.67	3.02	0.358	0.5496	
% body protein	14.54	1.34	14.80	0.86	0.358	0.5496	
Total body energy (MJ)	3106.84	633.22	3325.64	306.10	3.420	0.0644	.

B. CHANGES	All seals (n=14)		
	Mean:	Median:	SD:
Duration	189.79	183.00	23.00
Total mass change (kg)	13.14	8.00	20.22
Net water change (kg)	14.52	11.34	10.32
Net lipid change (kg)	-7.53	-12.53	15.10
Net protein change (kg)	5.47	4.42	3.72
Net water change (%)	5.35	5.72	4.52
Net lipid change (%)	-7.87	-8.41	6.65
Net protein change (%)	2.25	2.40	1.90
Net energy change (MJ)	-167.88	-278.77	591.59
Daily mass change (g)	66.25	40.67	105.85
Daily water change (g)	74.03	58.88	47.76
Daily lipid change (g)	-39.20	-60.18	82.23
Daily protein change (g)	27.95	24.31	17.07
Daily net energy change (kJ)	-887.68	-1437.97	3242.32

Table 3. Summary statistics based on individual measurements at the return for the first moult (A) and derived measures of changes occurring over the period between the midyear return and the moult. Relative lipid and protein energy indicate the proportions of the energy that is gained/lost as lipid and protein, and are calculated using energy densities of 39.5 and 23.5 kJ/g for lipid and protein respectively (Reilly and Fedak, 1990). Positive values indicate an increase while negative values represent a decrease. Changes in relative proportions are expressed in units of percent, for instance a change in lipid content from 40 to 30 % represents a decrease by 10 percent units.

Mass at the moult return (BM_{MLTR}) increased with BM_{MYR} (Median regression: $BM_{MLTR} = 73.48 + 0.60(BM_{MYR})$, $t_{1,12} = 3.266$, $p = 0.0068$), and since the slope was significantly less than one ($t_{1,12} = -2.207$, $p = 0.0474$), seals that were larger at midyear gained relatively less over the period leading up to the moult (Figure 5B). All three seals that lost mass over the period were larger than the average of the 14 seals. Seals that had a longer period between the two captures tended to return with lower BM_{MLTR} (Figure 5C). This relationship was not significant however, due to one extreme outlier with relatively high BM_{MLTR} and the longest DUR_{MM} (~ 1 month longer than the second longest DUR_{MM}). In agreement with the negative relationship between BM_{MYR} and DUR_{MM} , and the positive relationship between mass at both returns, the relative mass change ($MCHG_{Rel}$) increased with duration (Median regression: $MCHG_{Rel} = -62.58 + 0.36(DUR_{MM})$, $t_{1,12} = 4.977$, $p = 0.0003$), and again the three (large) seals that lost mass had relatively short durations (Figure 5D).

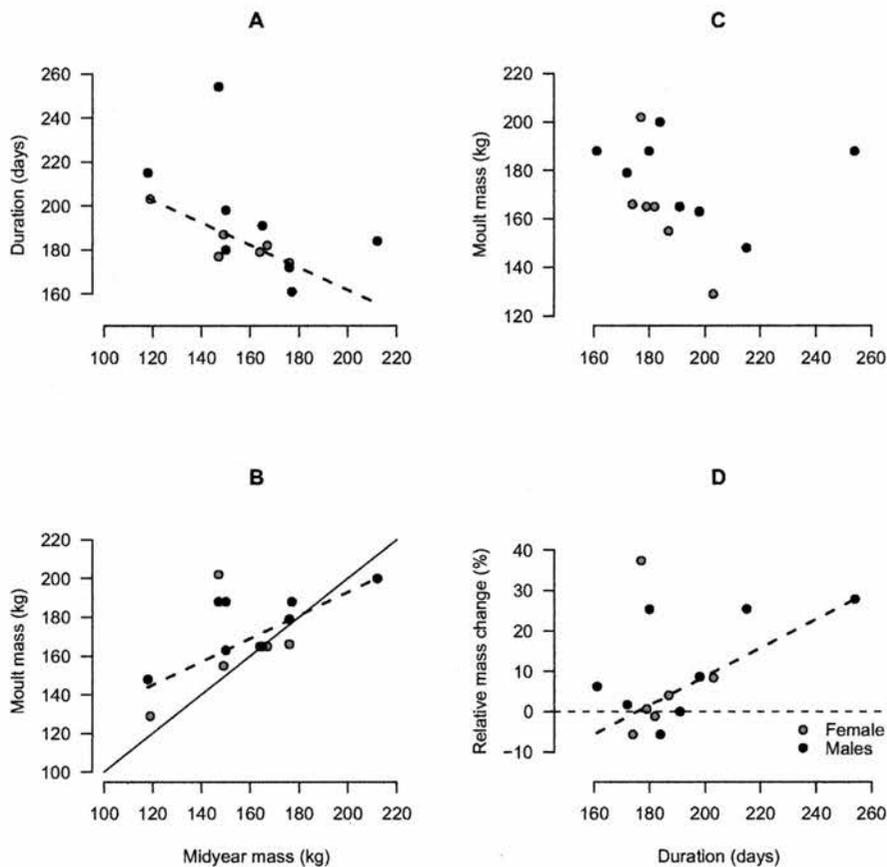


Figure 5. Relationships between body mass at the midyear and moult returns, and the length of the period (in days) between these two returns. The independent (x) variable in A and B is midyear mass, while in C and D duration is the independent variable. Broken lines represent fitted median (50% quantile) regressions, and the solid line in B) represents the 1:1 relationship between body mass at the two returns.

The body composition changed considerably between the midyear and moult returns.

In general, smaller seals showed greater increases in all components compared to larger seals (Figure 6). All seals except one increased their total protein, and the change ranged from -1 to 14.23 kg (5.47 ± 3.72 kg, Table 3B). This change was negatively related to midyear protein content ($\Delta TBP = 17.4 - 0.61(TBP_{MIR})$, $F_{1,12} = 7.742$, $r^2 = 0.34$, $p = 0.0166$, where ΔTBP denotes the change in absolute protein

content, and TBP_{MYR} is the midyear protein content (both in kg), see Figure 6A). In contrast, ten of the seals lost substantial amounts of lipid, while four seals gained lipid. Again, this change decreased significantly with increasing midyear lipid content ($\Delta TBF = 49.02 - 0.79(TBF_{MYR})$, $F_{1,12} = 12.96$, $r^2 = 0.48$, $p = 0.0036$, where ΔTBF denotes the change in lipid content (in kg) and TBF_{MYR} is the midyear lipid content, Figure 6B). Finally, this pattern was even more apparent when lipid was expressed as a proportion (Figure 6C). Only two seals (both males) increased their $\%TBF$ between midyear and moult, and again the magnitude (expressed as percent units) of the change was negatively related to the relative lipid content at midyear ($\Delta \%TBF = 15.34 - 1.05(\%TBF_{MYR})$, $F_{1,12} = 25.51$, $r^2 = 0.65$, $p = 0.0003$)

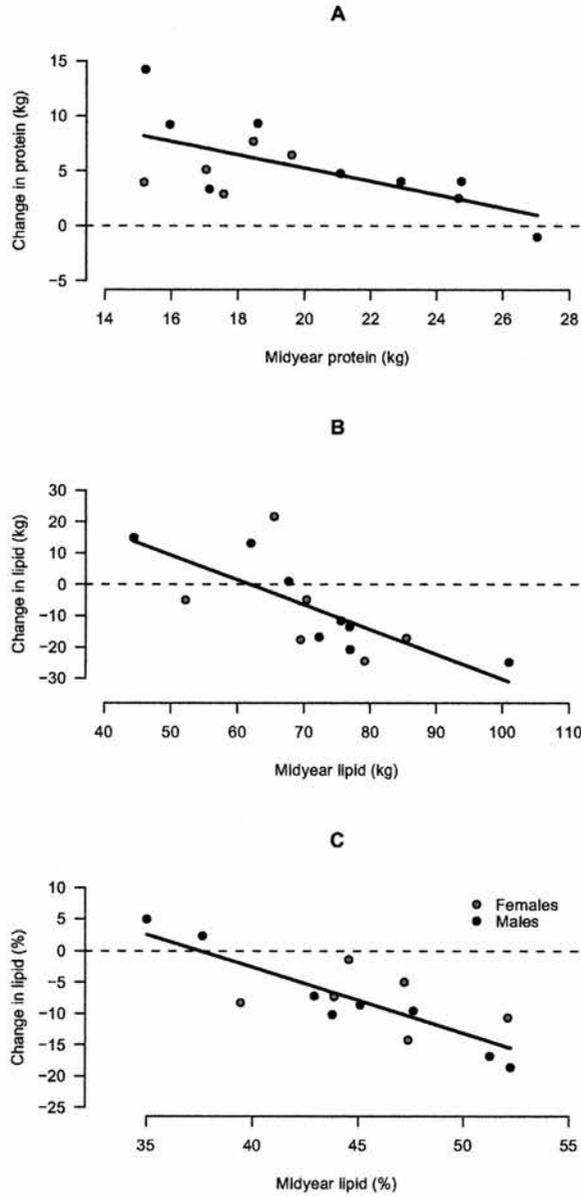


Figure 6. Relationships between body composition at the midyear return and the absolute change between midyear and moult. A) Total amount body protein, B) Total body lipid, and C) The relative lipid content. Here, the change indicated on the y-axis is expressed in units of percent, for instance a change in lipid content from 40 to 30 % represents a decrease by 10 percent units. Fitted lines are simple linear regressions (see text for regression results).

Body condition and probability of re-sight

The haulout pattern of individual seals known to have survived their first year (i.e. that had been sighted at least once after the first moult, referred to as SET 2 in the methods section) varied between the midyear and moult haulouts, and was also strongly affected by body size and, to some extent, gender. Results from generalized linear logistic models of probability of re-sight as a function of weaning mass and pup sex are presented in Table 4.

A: Resighting model; midyear haulout						
	Model structure	logLik	nPar	AIC	dAIC	AICw
All marked individuals	MYR ~ log(Wmass)	-1669.764	2	3343.529	0	0.655
	MYR ~ log(Wmass) + Sex	-1669.256	4	3346.511	2.983	0.147
	MYR ~ log(Wmass) * Sex	-1666.963	6	3345.925	2.397	0.198
Known survivors	MYR ~ log(Wmass) + Sex	-1091.83	4	2191.659	0	0.481
	MYR ~ log(Wmass) * Sex	-1090.361	6	2192.722	1.062	0.283
	MYR ~ log(Wmass)	-1094.541	2	2193.081	1.422	0.236
B: Resighting model; moult haulout						
	Model structure	logLik	nPar	AIC	dAIC	AICw
All marked individuals	MLTR ~ log(Wmass) * Sex	-1551.247	4	3110.494	0	0.802
	MLTR ~ log(Wmass) + Sex	-1553.647	3	3113.294	2.799	0.198
	MLTR ~ log(Wmass)	-1565.009	2	3134.018	23.52	0
Known survivors	MLTR ~ log(Wmass) * Sex	-1084.09	4	2176.18	0	0.907
	MLTR ~ log(Wmass) + Sex	-1087.418	3	2180.835	4.655	0.089
	MLTR ~ log(Wmass)	-1091.51	2	2187.021	10.84	0.004

Table 4. Summary of models describing the probability of re-sight of seals at A) the midyear haulout and B) the first moult. Models are ordered by their AICw values, from highest to lowest model probability. See text for further details.

When all seals that had initially been individually marked were included in the analysis (1243 females, 1222 males), the probability of re-sight ($P(\text{resight})$) during the midyear haulout increased significantly with weaning mass (GLM; $\text{logit}(P(\text{resight})) = -3.58 + 0.67(\log(BM_W))$, $AIC_w = 0.65$; ANOVA: $F_{1, 2463} = 15.98$, $p < 0.0001$), from ~ 0.2 at 50 kg to ~ 0.5 at 200 kg (Figure 7). We found no evidence that this relationship varied between males and females (GLM additive model: $AIC_w = 0.15$, ANOVA_{Sex}: $F_{2, 2462} = 15.98$, $p < 0.35$; interaction model: $AIC_w = 0.15$, ANOVA_{Interaction}: $F_{3, 2461} = 2.29$, $p < 0.13$, Figure 7). In contrast, for the seals that were known to be alive (861 females, 771 males), $P(\text{resight})$ decreased significantly with weaning mass (ANOVA_{BMW}: $F_{1, 1630} = 11.96$, $p = 0.0005$), from ~ 0.8 at 50 kg to ~ 0.5 at 200 kg (Figure 7). There was also support for higher $P(\text{resight})$ in males than females (GLM, additive model; $\text{logit}(P(\text{resight})) = 4.50 - 0.84(\log(BM_W)) + 0.24(\text{Sex}_M)$, $AIC_w = 0.24$, ANOVA_{Sex}: $F_{2, 1629} = 5.26$, $p < 0.022$, Figure 7). The slope also appeared to be slightly more negative in females (Figure 7). Although the inclusion of an interaction term did not significantly improve the fit (ANOVA_{Interaction}: $F_{3, 1628} = 1.05$, $p = 0.305$), the AIC weights indicate that the additive model was only 1.7 times more likely than the interaction model.

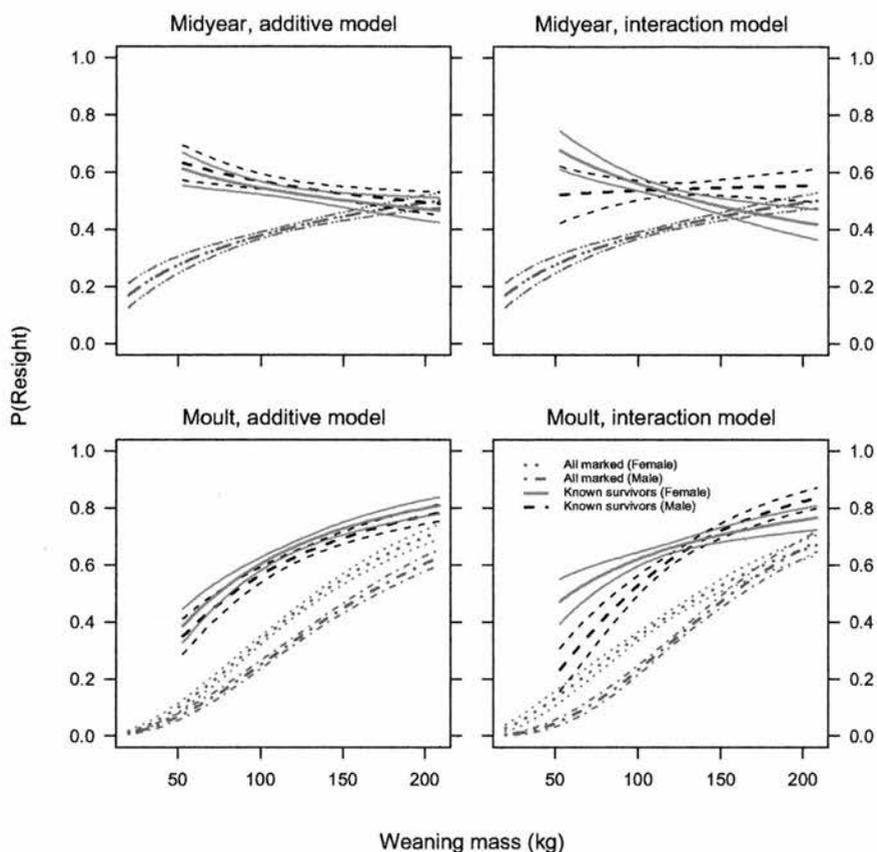


Figure 7 Probability of seals returning to, and being observed, at the midyear haulout (top graphs) and the moult (bottom graphs) in relation to weaning mass. The fitted curves are logistic GLM's, and the model comparisons and statistics are presented in Table 5. The blue curves represent models fitted to data from all animals that were initially marked and weighed at weaning in 1998 – 2000 (referred to as Set 1 in the text), while the red and black curves were fitted using a subset of seals that were confirmed to have been alive at these times (i.e. were seen at least once after the end of the first moult). See methods and results for further details.

The pattern was very different for the moult haulout. When all initially marked seals were included, $P(\text{resight})$ increased with weaning mass for males and females, and in this case the best model included an interaction term between weaning mass and gender (GLM, interaction model; $\text{logit}(P(\text{resight})) = -8.98 + 1.81(\log(BM_W)) -$

$4.55(\text{Sex}) + 0.86(\text{BM}_W * \text{Sex}_M)$, $AIC_w = 0.80$, $\text{ANOVA}_{\text{Interaction}}: F_{3, 2461} = 4.80$, $p < 0.028$, Figure 7). In general, $P(\text{resight})$ increased from ~ 0.1 at 50 kg to 0.7 at 200 kg. In contrast to the midyear haulout, females had higher $P(\text{resight})$ values than males, especially for weaning masses below ~ 100 kg (Figure 7). This pattern was even more striking when only the known survivors were analysed (GLM, interaction model; $\text{logit}(P(\text{resight})) = -5.89 + 1.31(\log(\text{BM}_W)) - 6.61(\text{Sex}_M) + 1.32(\text{BM}_W * \text{Sex}_M)$, $AIC_w = 0.91$, $\text{ANOVA}_{\text{Interaction}}: F_{3, 1628} = 6.65$, $p < 0.010$, Figure 7). For seals with high weaning masses, the $P(\text{resight})$ was similar for males and females at ~ 0.8 , but while it decreased slightly with weaning mass this decrease was very steep for males. While $P(\text{resight})$ for small females (~ 50 kg) was $\sim 0.3 - 0.4$, the corresponding values for males of similar weaning masses was only ~ 0.1 .

Body condition and first-year survival

First-year survival probability, $p(S)$, was related in a relatively complex way to the individual weaning covariates, and summary data for the tested models are presented in Table 5. The survival probability increased with total body mass (Logistic GLM, $F_{1,99} = 6.136$, $p = 0.0132$), and while the model was not improved significantly by including gender as an additive effect ($F_{2,98} = 2.316$, $p = 0.1280$), there was a significant interaction between mass and gender ($F_{3,97} = 9.134$, $p = 0.0025$). Based on AIC weights, this interaction model was the most parsimonious of the models that included body mass (BM) as the main size index (Table 5A), and suggests that while $p(S)$ was not related to BM for females, there was a significant positive relationship for males (Figure 8A). The inclusion of relative lipid content ($\%TBF$) by itself along with BM did not improve the model ($F_{2,98} = 0.019$, $p = 0.8901$). However, the

model including the gender factor along with *BM* and *%TBF* as covariates was the second-best model in this set (Table 5A).

A. Mass & lipid models	LogLik ¹	Npar ²	Df ³	AIC ⁴	DAIC ⁵	AICw ⁶
Mass + Sex + (Mass * Sex)	-61.091	4	97	130.181		0.598
Mass + Lipid + Sex + (Mass * Sex) + (Lipid * Sex)	-59.566	6	95	131.132	0.950	0.372
Mass	-66.816	2	99	137.632	7.451	0.014
Lipid + Sex + (Lipid * Sex)	-65.121	4	97	138.242	8.060	0.011
Mass + Lipid	-66.807	3	98	139.613	9.432	0.005
B. Lean & lipid models	logLik	nPar	Df	AIC	dAIC	AICw
Lean + Lipid + Sex + (Lean * Sex) + (Lipid * Sex)	-59.402	6	95	130.804		0.899
Lean + Sex + (Lean * Sex)	-63.924	4	97	135.847	5.043	0.072
Lean	-67.361	2	99	138.721	7.917	0.017
Lean + Lipid	-66.799	3	98	139.599	8.795	0.011

C. Summary of best scoring model

Model parameter	Coefficient		
	Mean	S.E.	Deviance z p
Intercept	2.065	3.350	0.617 0.5376
Lean	0.007	0.018	5.047 0.400 0.6893
Lipid	-0.066	0.064	1.123 -1.028 0.3040
Sex	-19.040	6.293	2.379 -3.026 0.0025 **
Lean * Sex	0.092	0.039	4.327 2.386 0.0170 *
Lipid * Sex	0.299	0.113	8.088 2.648 0.0081 **

Model Goodness-Of-Fit (χ^2 df=95)

118.804 0.0497 *

¹ $-2(\log\text{-Likelihood})$ ² Number of parameters ³ Degrees of Freedom ⁴ Akaike Information Criterion ⁵ AIC difference between candidate model and "best" model ⁶ AIC weight (see methods section)

Table 5. Summary of tested models describing the probability of first-year survival in relation to body mass and composition (relative lipid content). A) models using total body mass as the fundamental index of pure body size, B) models using total lean (i.e. lipid-free) mass as the size index.

Models are ordered by their AICw values, from highest to lowest model probability. C) summary table of the highest model. The test statistics and p values in C) refer to the significance of each term coefficient in the final ("best") model.

While none of the terms including *%TBF* were significant, the AIC weights suggested that the top-scoring (simpler) model was only ~ 1.6 times more likely than the second-best (more complex) model (AICw = 0.598 and 0.372 respectively).

The non-significance of the *%TBF* is most likely due to some degree of collinearity with *BM*, since body mass is a combination of lean and lipid tissue. We therefore tested a series of models that used lean body mass (i.e. $LBM = BM - TBF$) instead of *BM* (Table 5B). The most parsimonious model contained *LBM* and *%TBF* as covariates along with gender interactions. In this case, the evidence in support of the best model was very convincing. Based on AIC weights, it was more than 12 times more likely than a model that did not contain the *%TBF* term (AICw = 0.899 and 0.072 respectively, Table 5B). The effect of *%TBF* was not significant in itself ($F_{2,98} = 1.123, p = 0.2893$), but there was a highly significant interaction between *%TBF* and gender ($F_{2,98} = 8.088, p = 0.0044$). The summary statistics and statistical tests of final parameter estimates are shown in Table 5C. This model suggested that, in agreement with the body mass model, $p(S)$ was not related to *LBM* in females, but increased significantly with *LBM* in males (Figure 8B). However, while $p(S)$ increased significantly with *%TBF* in males, there was a significant negative relationship between $p(S)$ and *%TBF* for females (Figure 8C).

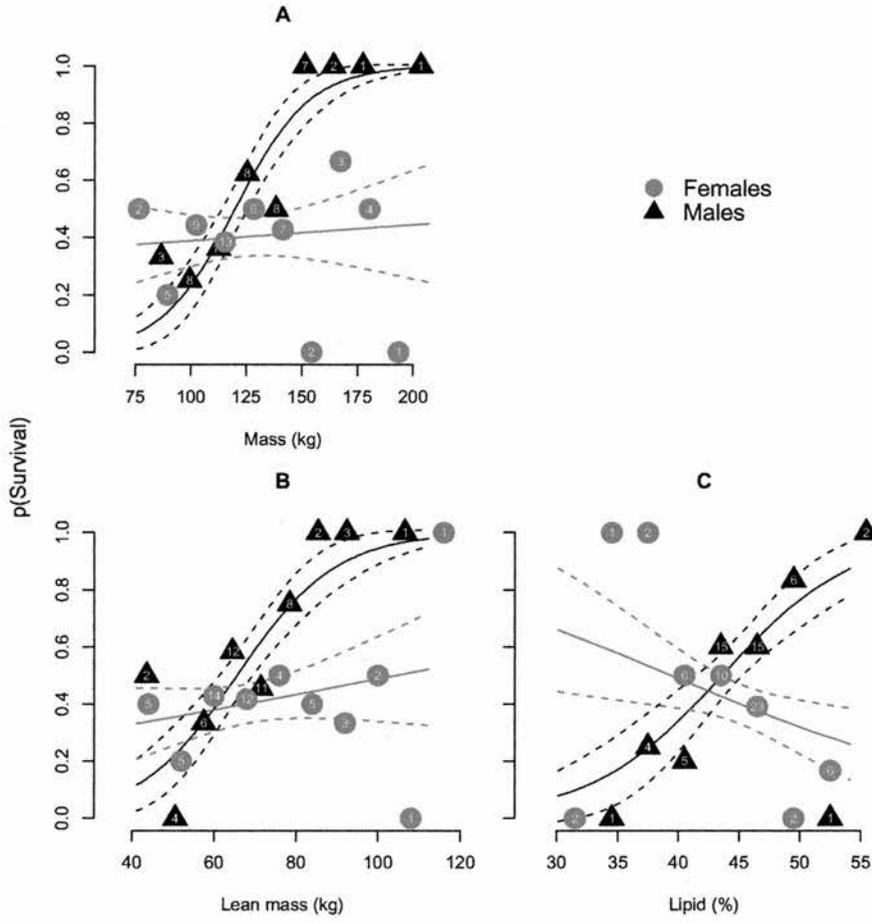


Figure 8. First-year survival probability as a function of A) total body mass, B) lean body mass, and C) percent body lipid. The curves in each plot represent the probability of survival predicted from logistic Generalized Linear Models including each explanatory variable (mass, lean mass and percent lipid respectively) along with gender. Solid symbols represent the proportion of individuals within equal-sized bins along the x-axis that were seen at least once after the first moult (at ~ 12-14 months age). These proportions are only included for visual comparison to the fitted curves, and were not used in the model fits. Numbers within the symbols indicate the number of data points used to calculate these proportions. See results section for further details on model selection and testing.

Discussion

In this study, we have provided longitudinal data on individual changes in mass and body composition of southern elephant seal pups over the year after they first leave their natal beaches. To our knowledge, this is the first study in a marine mammal that examines the effects of variations in early body composition (a proxy for maternal investment) on the fate of individuals during the critical first period of nutritional independence. We have shown that variations in the material and energy provided during the short lactation period can have an important influence on growth and utilisation of body components that last well beyond the initial fasting period on land. We have also shown that body composition (and not only absolute body size) can have a strong influence on the probability that individual seals survive their first year, and this also appears to be dependent on the individual's sex. We have thus expanded several earlier studies that describe the energy expenditure of phocid pups during the post-weaning fast, before they go to sea for the first time and provided novel and important information that will help improve our understanding of the complex links and tradeoffs between maternal investment of a mother, her future survival and reproductive success, and the potential return on her investment in terms of the survival and recruitment of offspring into the breeding population.

General summary of changes during the first year

Previous studies on southern elephant seals pups (Bell et al., 1997; Bryden, 1972) have shown that their overall body size increases substantially over the first year at sea. This has mainly been attributed to somatic growth, and it is believed that seals

therefore become progressively larger but leaner during this year. Although our results generally confirm this (Figure 1A&B), they also suggest that the growth of different components may vary over time and between individuals, as a result of variations in the assimilation and synthesis of different body components. During the first foraging trip in this study (autumn and early winter), seals increased their lean body as well as their absolute lipid reserves, while the change in relative body composition did not follow a consistent trend (Figure 1C). While the growth in lean tissue appeared to continue along a similar trajectory over the period between the midyear and the first moult (late winter – early spring), the rate of lipid accumulation was significantly reduced, and the relative lipid content at the moult was noticeably lower than at any previous point during the first year (Figure 1C, also compare Figure 3B and 6C). These changes may be the result of inherent, hormonally controlled growth requirements and the need to take onboard extra protein in preparation for the moult, during which elephant seals have to synthesize a complete new layer of outer epidermis and hair (Ling, 1965). However, the apparent reduction in the assimilation of lipid stores (also an important prerequisite for a continuous terrestrial fast) may have been augmented by a gradual reduction in food availability over the winter months, preventing seals from accumulating lipid stores at the same rate during late winter. Recent satellite data from some of the pups in this study that were tracked over consecutive trips during the first year (SMRU, unpublished data), appear to lend support to this suggestion. Telemetry data from individual pups tracked over consecutive trips suggest that some individuals that returned to a feeding area that was successfully visited during the first trip, appeared to accumulate much less lipid during this second visit (indicated by a negative change in drift rate over this

second trip, see Biuw et al., 2003). Furthermore, a few individuals that returned to Macquarie for a midyear haulout in late winter were in noticeably poorer condition (SMRU unpublished data). However, this is still speculative, and needs to be verified with more data on at-sea behaviour of seals with known body compositions before and after the trip. We should also point out that the observed reduction in lipid accumulation from the first to the second trip is probably somewhat biased, since it is measured over a period that includes the midyear haulout fast. If instead the changes had been measured between the end of this fast and the moult return, it may have been more similar to the changes observed over the first trip. However, this is unlikely to account for the entire difference observed between these two periods, since the midyear haulout is relatively short (average ~ 14 days, Wheatley, 2001).

One noticeable trend throughout the first year was that smaller seals performed consistently better, in relative terms, with greater proportional growth and energy accumulation, compared to larger pups (see Figures 2C, 3B, 4B and Figure 6). This pattern may be the result of several mechanisms operating simultaneously over this critical transition to independent foraging. Firstly, a larger lean body requires higher absolute metabolic rates (Kleiber, 1975), and therefore higher absolute energy requirements. Smaller seals therefore do not need to assimilate the same quantities of energy and material as larger seals to cover their daily maintenance requirements and to grow. If all seals were to have access to similar food resources, and if foraging ability were not related to body size, smaller seals could have greater potential for growth and will show relatively greater increases in body reserves. Recent telemetry data (McConnell et al., 2002) and SMRU, unpublished data), suggests that there

are no consistent differences in foraging areas used by Macquarie Island pups of different body size, so that on a geographic scale they probably have access to similar resources. In terms of their access to vertically distributed prey, several studies have shown that the diving ability of young elephant seals is strongly influenced by body size (e.g. Hindell et al., 1999; Irvine et al., 2000), and suggest that larger seals can remain longer at underwater prey patches. It is currently unknown to what extent this influences the prey encounter rates, but it is possible that this is of significance only in areas of low prey density and/or accessibility (due to for instance deep vertical distribution).

One other, potentially more important, explanation for the relatively higher growth rates of smaller pups may be the fact that early survival appears to be size-dependent. As suggested by previous studies (McMahon et al., 2000b, 2003), and further supported by this study, larger seals have a generally higher probability of surviving their first year (although this may vary between the sexes, see results and discussion below). Therefore, if smaller seals are under more severe constraints in terms of energy reserves, it is very likely that while successful foragers within this size range survive (and return), unsuccessful individuals die of starvation while at sea. In contrast, less successful foragers within the larger size range may still be able to survive by relying to some degree on stored reserves, and may therefore return to land in relatively worse condition. This tendency, as was also postulated by Irvine et al. (2000), could potentially explain the greater increases in size and body condition of smaller seals presented in this study.

In this context, it is also important to consider the observed differences between male and female pups. More than 75 % of the females in our sample increased their relative lipid content between departure and the midyear return, while a smaller proportion of males (63 %) showed a positive change (Figure 4B). Biuw et al. (In Prep.) found that male and female pups allocated their resources differently during the post-weaning fast, and while they had similar body compositions at weaning, females were relatively fatter than males at the end of the fast. Interestingly, we found no such differences at departure among the pups that eventually returned for the midyear haulout. This apparent inconsistency may be related to the different relationships between body size/condition and resight and survival rates between the sexes (Figures 7 & 8). Among pups that were known to have survived to at least ~1.5 years of age, the probability of female pups returning for the midyear haulout decreased with increasing weaning mass, while there was some indication that the reverse was true for male pups (Figure 7, top right). While males returning for the midyear haulout may be representative of the total sample of pups measured before departure, larger females from the departure capture are under-represented at the midyear return. Because of the relatively greater increases in size (and lipid content) among initially smaller seals, this somewhat skewed pattern of return may partly explain the relatively larger lipid increases observed among females than among males.

Irrespective of which is the most plausible explanation, there are some important and interesting consequences of these patterns. While large initial energy reserves may provide an important buffer that increases an individual's probability of surviving their first year, the longer-term benefits may not be as significant, since survivors

among the smaller size classes are able to essentially “catch up” on the larger-sized seals in terms of growth and energy assimilation during the first year. This may explain some of the results from previous survival studies. While McMahon et al. (2003) showed that large body mass at weaning has a positive effect on the first-year survival of elephant seals at Macquarie, they also observed that this influence is diminished over the following two years. In the longer term, these patterns may also have important implications for the selection forces acting on individual seals, and thereby the evolution of the maternal strategies displayed by this species. For instance, Fedak et al. (1996) found that while small mothers can only produce small pups, large mothers can produce large pups at only moderate expenditures, or could potentially produce extremely large pups at a higher cost. However, there appears to be an upper limit on the resources expended by large mothers. Instead of producing extremely large pups, they reduce their relative expenditure, and thereby presumably increase their potential future reproductive success. Such a strategy may indeed be appropriate if, as our data and previous research suggests, the link between early body condition of offspring and the long-term benefits in terms of their reproductive success is weak, once they have survived their critical first year. However, the exact shape of this function will also be pertinent. For instance, where along the range of investments (weaning mass or condition) do the greatest rate of increase/decrease in first-year survival occur, and how is this influenced by external factors such as annual variations in prey density and distribution?

Differences between females and males

Our results suggest that among pups that survive the transition to nutritional independence, there are differences in the way body composition changes in male and female pups. More than 75 % of the females in our sample increased their relative lipid content between departure and the return for the midyear haulout, while a smaller proportion (63 %) of males showed a positive change (Figure 4B). Biuw et al., (In Prep.) found that male and female pups allocated their resources differently during the post-weaning fast, and while they had similar body compositions at weaning, females were relatively fatter than males at the end of the fast. Despite the fact that many of the pups in the sample studied here were also examined in the earlier study, we found no such differences between male and female pups. This apparent inconsistency can be resolved by examining the differences in probabilities of pups returning for the midyear haulout in relation to body size at weaning. Among pups that were known to have survived to at least ~1.5 years of age, the probability of female pups returning for the midyear haulout decreased with increasing weaning mass, while there was some indication that the reverse was true for male pups (Figure 7, top right). This suggests that, while males returning for the midyear haulout are representative of the total sample of pups measured before departure, larger and potentially fatter females from the departure capture are under-represented at the midyear return. However, given this slightly skewed pattern of return, it is interesting that females again accumulated relatively larger lipid stores than males. Consequently, while there was no significant difference in the change in mass of male and female pups, males had a significantly greater change in total protein content and hence, lean body size, over the first trip.

Body condition and first-year survival

Age-specific survival is one of the two fundamental parameters that determine an animal's fitness, the second being age-specific fecundity (Clutton-Brock, 1988; Houston and McNamara, 1999). There has been much progress recently in constructing life-history tables of these parameters for southern elephant seals (e.g. McMahon, 2002), but many details about the way these parameters vary in relation to maternal investment in offspring and the way in which individuals allocate the received energy into growth and reserves are still unknown. We have attempted to provide some additional insights into these mechanisms by extending the analyses of first-year survival to include body composition in addition to simply mass. Our results suggest that first-year survival $p(S)$ in male pups is very strongly related to body size as well as body composition at weaning, but that the pattern among female pups is more variable and much less consistent (Figure 7). The fact that we find a strong positive correlation between $p(S)$ and total body mass in males is not surprising. This is the pattern we would expect, given that large body reserves may allow seals to survive longer before they have to find and capture prey. This pattern is also consistent with previous research (McMahon et al., 2003). Furthermore, it appears that males in our study benefited from larger lean mass as well as relatively larger lipid energy reserves (Figure 7 B&C). The correlation with lean mass appears to be consistent with the suggestions made by Biuw et al. (In Prep.) (see also discussion above), that acute protein depletion may be more critical than lipid depletion. The fact that the effect of large lipid reserves was still significant after lean mass had been controlled for suggests, not surprisingly, that seals with large relative lipid stores

on top of a large lean body enjoy the best of both conditions, and will have the best chances of surviving the initial transit period to the feeding grounds. While protein sparing is recognized as an important adaptation for fasting, it may also have implications for animals that are feeding, but not in positive energy balance.

The pattern for females is less conclusive and somewhat confusing. First-year survival appeared to be unrelated to body mass and only a weakly (if at all) positively related to lean mass. This is not an artefact of the differential return rates described earlier, since $p(S)$ is defined as seals being observed at least once *after* the end of the first-year moult. However, if females (especially those with large energy reserves) have a greater tendency than males to stay away from their natal island over the first couple of years, there is a possibility that a pattern like the one observed here could arise. Because our two birth cohorts (1998 and 1999) were only in their 3rd and 4th year respectively during the last year of re-sights available to date (2002), it is possible that differential return rates of males and females over their first 3-4 years of life may have biased our analyses. However, a rough analysis of the age at which animals are first seen after leaving the island suggests that the distribution is very similar for males and females. However, because of the amount of work required to obtain measures of body composition, our sample size is relatively small compared to earlier studies of survival, and more data on body composition and survival will be needed before we can confirm or reject these results, and our analyses therefore have to be considered preliminary at this stage. With this in mind, we can nevertheless speculate as to possible reasons for the observed pattern in females. There was a slight tendency for $p(S)$ to increase with increasing lean mass, which may again be explained by the

critical importance of protein during the early phase of the first foraging trip (Biuw et al., In Prep.). Since our results indicate that females in general have a tendency to conserve lipid to a greater extent than males by increasing their energetic contribution of protein to sustain metabolism, it is possible that fatter females are depleting their smaller protein stores at a relatively higher rate, and therefore may risk approaching acute protein levels before they have reached suitable foraging areas. Although this is again speculation, it may serve to point out areas where much more research is needed to fully understand the development of maternal strategies in elephant seals and other phocids.

Body condition and at-sea behaviour

Elephant seals remain at sea for several months, and it is only possible to obtain point measurements of individuals when they return to the haulout. These point measurements give information only on the net changes over the entire trip to sea, but do not tell us anything about the rate at which seals utilise their stored reserves, or when and how they acquire energy and material on a day-to-day basis while at sea. Recent analyses of satellite telemetry data (some of which were collected from a subsample of the pups in this study) have provided indirect but virtually continuous measures of the changes in relative body composition throughout the at-sea migrations (Biuw et al., 2003). Using these data in combination with the information on net changes in body composition over the entire trip, we have attempted to create a simple model of the links between body condition, at-sea behaviour and daily energy requirements and acquisition.

The significant negative relationship between trip duration and relative mass gain is probably caused by differences in movement patterns and foraging success between individuals. These differences may in turn be linked to physiological factors such as body composition and energy expenditure and allocation of body reserves. Such potential links have previously been discussed by for instance Biuw et al. (2003) Hindell et al. (1999), Irvine et al. (2000) and McConnell et al. (2002). The most successful individuals (in terms of the net assimilation of energy and material) are most likely those that 1) spend relatively less time at sea in transit to, between, and from suitable feeding areas and 2) once on these feeding areas, are able to find and capture prey and efficiently assimilate the material and energy into growth and body energy reserves. The period of initial transit from the haulout site until seals have found suitable feeding grounds is likely to be the most critical period, especially in young naïve pups that have already spent a considerable amount of time fasting after weaning before they go to sea for the first time, and given that they have to find suitable feeding areas apparently without any guidance from older conspecifics. In comparison with other important breeding sites for southern elephant seals, Macquarie Island is located relatively far to the north of the presumed main foraging areas around and to the south of the Polar Front (Field et al., 2001; McConnell et al., 2002), and elephant seals from Macquarie therefore have to travel far before they are likely to find suitable prey. Based on daily travel rates and movement patterns, McConnell et al. (2002) showed that elephant seal pups from Macquarie, tracked using satellite telemetry, travelled fairly rapidly and in a directed manner (Phase 1) for about 30 days to locations more than 1000 km from the island before they switched to a behaviour pattern indicative of active searching or feeding (Phase 2). This was supported in a

study by Biuw et al. (2003) that used dive characteristics to calculate changes in buoyancy (and estimate relative lipid content). Their results suggest that few seals were increasing their relative lipid reserves before ~ 30-50 days after departure, although some individuals may have started feeding successfully slightly earlier. Figure 9 illustrates these main patterns for seals used in the study by Biuw et al. (2003).

In an attempt to estimate how much of the available energy reserves seals utilise during Phase 1, McConnell et al. (2002) calculated the days to starvation for newly weaned pups based on calculated estimates of body composition at weaning and estimates of the rate of utilisation of body materials while fasting. They suggested that while large pups have sufficient reserves to sustain them until the transition from Phase 1 to Phase 2, small pups could be approaching critical limits (in lipid, protein or both depending on the relative energetic contribution) at or before this transition. These ideas were further developed by Biuw et al. (In Prep.), based on actual individual measurements of changes in body composition of pups while fasting on land. Their calculations suggest that absolute body size and energy stores are less important than the rates of depletion of the various body components, and that despite the general pattern of phocids deriving most of their energy while fasting from lipid, protein depletion may be the most critical limiting factor. Pups are likely to die from acute protein depletion before their lipid reserves have reached critical levels, and this may occur within a couple of weeks for pups that rely to even moderate degrees on protein catabolism (for instance ~ 10% of energy derived from protein while fasting, Biuw et al., In Prep.).

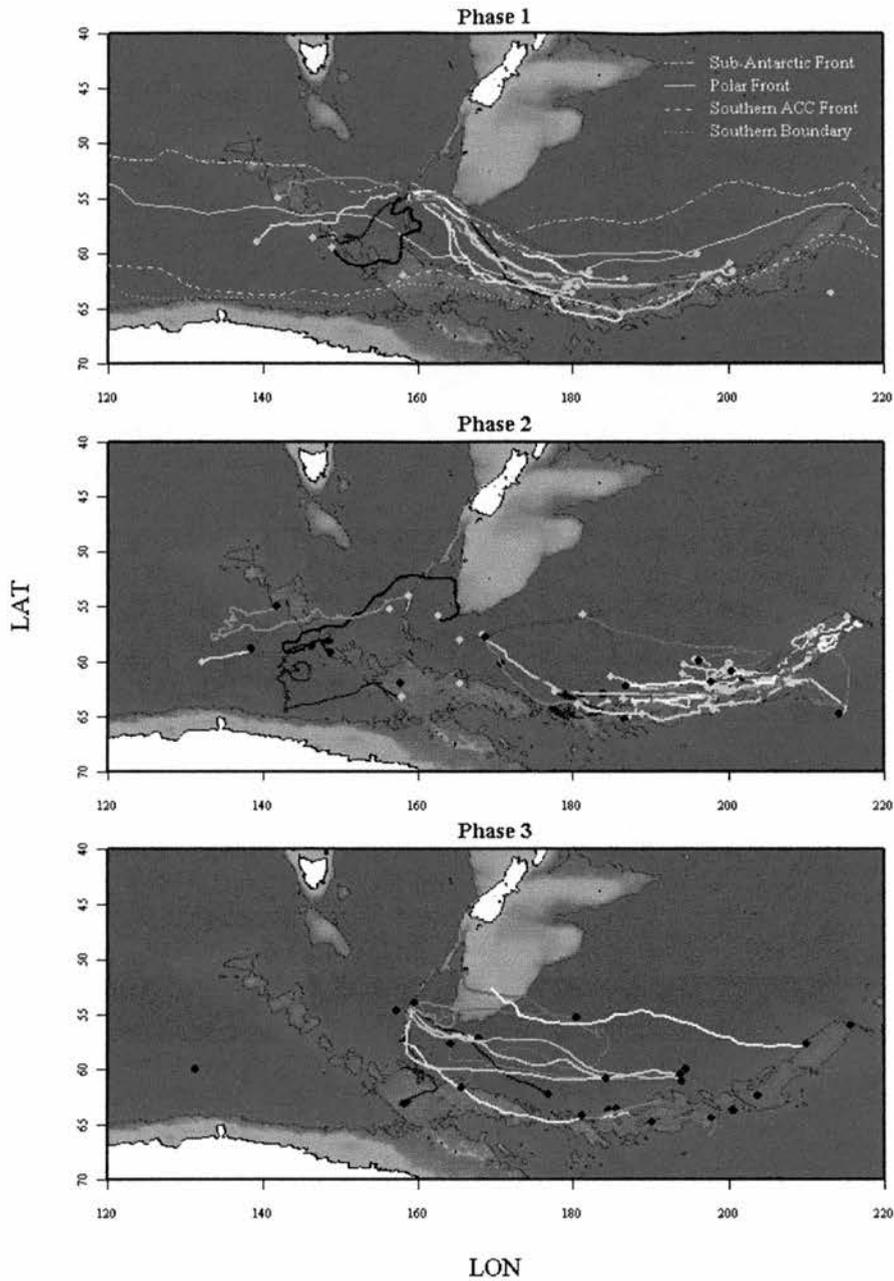


Figure 9. Maps showing the spatial distribution of 20 newly weaned elephant seal pups from the 1996, 99 and 2000 cohorts, during the three main phases of their first foraging migrations away from Macquarie Island. Black dots represent the at-sea starting location for a given phase, while yellow dots represent the end location. Transitions between Phase 1-2 (2-3) were defined as the first (last) day where a seal showed a negative (positive) change in drift rate. These results were based on data presented in (Biuw et al., 2003). The white lines in the top map represent the major fronts and boundaries within the Antarctic Circumpolar Circulation (ACC), based on (Orsi et al., 1995). The Southern Boundary refers to the southern boundary of the ACC.

At first glance, these results are inconsistent with the suggestions by Biuw et al. (2003), who concluded, based on changes in buoyancy measured from dive characteristics, that seals in their study were unlikely to have reached critical levels of body reserves before the end of Phase 1. This conclusion assumed that buoyancy is a good index of the depletion/accumulation of lipid reserves and, although their simulation tests suggested that this is the case, their method cannot be used to estimate the absolute amounts of lean tissue or the rate at which protein is depleted or assimilated. This is a crucial point, because of the different functions of lipid and protein in the body. Lipid has a dual function, providing thermal insulation while also being the main energy reserve (Bryden, 1964). The value of lipid to an animal is therefore a function of what fraction of the body is lipid and acute effects (for instance increased thermoregulatory costs or eventually severe hypothermia) are therefore assumed to occur when animals have reached some threshold of relative lipid content (for instance 10 % of body mass, see Cahill et al., 1979). The pattern is very different for protein. Because the overall growth of an animal depends on the accumulation of lean tissue rather than lipid, and because most of the essential body organs consist to a large part of protein, the “value” of protein to an animal is determined more by the absolute amount than the fraction of the body that it constitutes. Acute effects of protein depletion are therefore believed to occur when animals have lost some given proportion of their initial protein (for instance 30 %, Cahill et al. (1979), but see Biuw et al. (In Prep.) for elephant seals). Because of these differences, pups may be approaching acute levels of body protein towards the end of Phase 1 (as suggested by the estimated days to starvation in Biuw et al. (In Prep.)) while they still have relatively large lipid stores (as indicated by the buoyancy and estimated relative body composition in Biuw et al., 2003).

All seals in our sample increased their total energy content between departure and the return for the midyear haulout, but the magnitude and relative composition of this increase varied considerably between individuals. At the lower end of energy increase, seals gained an absolute amount of roughly 600 MJ (although one seal had a similar amount of energy at return as at departure). Almost all of these pups showed a considerable decrease in relative lipid content, and the increase in energy content was therefore caused by increases in total protein (and overall lean tissue). In contrast, seals at the upper end were able to increase their energy content by a factor of almost 1.5 times, i.e. the absolute energy content at return was almost 2.5 times greater than at departure, irrespective of their initial energy content. This was caused by increases in total body size as well as substantial increases in relative lipid content (Figure 5A). The relative net gain in energy over the trip decreased with increasing trip duration. However, this relationship was entirely driven by the inverse relationship between trip duration and increase in overall body size (Figure 2), and the change in relative body composition did not vary with trip duration.

A simple energetic model

Because of the long period spent at sea, and further complicated by the considerable amount of time elephant seals spend travelling to and from feeding grounds, the changes in body composition and energy over the entire trip do not provide any estimates of daily energy intake while foraging. In this section, we have tried to develop a simple model by combining our data on individual condition changes with information on the migration patterns and inferred foraging behaviour collected using satellite linked data loggers deployed on newly weaned Macquarie Island elephant seals (Biuw et al., 2003; Hindell et al., 1999; McConnell et al., 2002). Some of these tracking data were collected on a sub-sample of seals also assessed for body composition in 1999. Body composition data were not collected during the first two deployments (1995 and

96). Furthermore the elephant seal program at Macquarie Island was unfortunately closed at the end of the breeding season in 2000, and consequently none of the pups from the 2000 cohort, whose body composition was known, could be recaptured during subsequent returns to Macquarie. This severely limits our sample size of animals with both body composition and telemetry data, and in the following modelling exercise we have therefore been forced to use a combination of individual and cross-sectional data. We hope that this section will illustrate the importance of detailed longitudinal data on known individuals for our understanding of the links between maternal expenditure, offspring body condition and energetics, at-sea behaviour, individual probability of survival and ultimately the effects on population dynamics.

In order to obtain approximate estimates of the rate of energy gain while foraging, we used the methods first outlined in McConnell et al. (2002) and later modified by (Biuw et al., In Prep.), to extrapolate the daily rates of mass and body water change over the post-weaning fast. This method requires data on mass and body composition change throughout the post-weaning fast in addition to body condition measurements upon the midyear return. These data were available for 27 of our seals. We calculated the approximate number of days our seals could survive at sea before their energy reserves would become critically depleted. If we assume that 1) pups have similar rates of depletion of energy and material when fasting at sea and on land, our pups would have reached acute levels of body stores after on average 33.3 days (50% inter-quantile range ~ 17 – 48 days). We calculated the energy content of seals at this depleted stage, and assumed a continuous foraging period of 100 days (see (Biuw et al., 2003)). In order for seals to achieve the energy content at midyear haulout observed in this study, these calculations resulted in estimated daily rates of net energy gain of about 8 – 40 MJ/day (50% inter-quantile range: 12.5 – 28.6 MJ/day). However, these estimates do not take account of the fact that seals probably do not

feed as much while in transit back to the haulout after the foraging period. As suggested by (McConnell et al., 2002) and (Biuw et al., 2003), the return transit of elephant seal pups back to Macquarie (“Phase 3”) lasts for about 35-40 days. Along with the data on observed trip durations, we therefore estimated the minimum duration of the foraging period by assuming that 1) seals start foraging just before they have depleted their energy stores, and 2) that they take 40 days to return to Macquarie. The estimated duration of foraging periods for our pups ranged from 145 to 169 days (101 ± 30.8 days), and this modification resulted in estimated daily net energy gains of $\sim 10 - 70$ MJ/day (50% inter-quantile range: $\sim 18 - 46$ MJ/day). We took this one step further, and assumed that while foraging, our pups expended energy at a rate similar to the diving metabolic rates measured for captive, freely diving grey seals (Sparling, 2003). In order to cover the daily energy expenditure and allow for the observed growth and accumulation of energy reserves, seals would need to have a gross daily energy intake of about $25 - 78$ MJ/day if we assume a 100-day foraging period, and $\sim 25 - 90$ MJ/day if we use the estimated individual durations of foraging periods. These values are similar to the average gross energy consumption of 77.3 and 43.2 MJ/day for male and female southern elephant seals respectively, estimated by (Boyd et al., 1994). Their values were calculated for each sex but across all age classes, and it is therefore slightly surprising that our values calculated for pups are of similar magnitudes. However, the estimates in Boyd et al. (1994) were based on theoretical calculations and assumptions about average body composition and energy expenditure, and are likely to be sensitive to errors in any of these assumptions. In comparison, based on heart rate and estimated oxygen consumption of a free-ranging elephant seal female, Hindell and Lea (1998) estimated a daily energy requirement of 101 MJ/day, suggesting that our approximate estimates may be reasonable for the smaller weaned pup in our study. Although our calculations are also based on several assumptions, they are nevertheless likely to provide slightly more accurate estimates.

If this is the case, the predicted biomass consumption estimates calculated by Boyd et al. (1994) may be underestimated.

Although these types of calculations necessarily involve several assumptions that need to be empirically verified and/or modified, they highlight the importance of detailed individual-based studies of energetics and behaviour of seals for our understanding of the links between ecosystem characteristics and population dynamics. Such models will also have to be made spatially explicit, so that we can relate age- and sex-specific seal distribution to the distribution and abundance of potential prey. Our field measurements of physiological state and energy consumptions need to be refined. One possible approach would be to estimate the relative body composition of seals from their drift rates using the methods developed in Biuw et al. (2003), and combine this with more extensive body composition measurements on land, and more exact measurements of the field metabolic rates of free-ranging seals.

References

- Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. In B. N. Petran and F. Csaki (eds.), *International Symposium on Information Theory*, pp. 267-281. AkadŠemiai Kiadi, Budapest, Hungary.
- Arnbom, T., M. A. Fedak, and I. L. Boyd. 1997. Factors affecting maternal expenditure in southern elephant seals during lactation. *Ecology*, 78:471-483.
- Arnbom, T., M. A. Fedak, I. L. Boyd, and B. J. McConnell. 1993. Variation in Weaning Mass of Pups in Relation to Maternal Mass, Postweaning Fast Duration, and Weaned Pup Behavior in Southern Elephant Seals (Mirounga-Leonina) At South-Georgia. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 71:1772-1781.
- Beck, C. A., W. D. Bowen, and S. J. Iverson. 2000. Seasonal changes in buoyancy and diving behaviour of adult grey seals. *Journal of Experimental Biology*, 203:2323-2330.
- Bell, C. M., H. R. Burton, and M. A. Hindell. 1997. Growth of southern elephant seals, Mirounga leonina, during their first foraging trip. *Australian Journal of Zoology*, 45:447-458.
- Biuw, M., B. McConnell, C. J. A. Bradshaw, H. Burton, and M. Fedak. 2003. Blubber and buoyancy: Monitoring the body condition of free-ranging seals using simple dive characteristics. *Journal of Experimental Biology*, 206:3405-3423.
- Biuw, M., K. E. Wheatley, J. R. Speakman, H. R. Burton, and M. A. Fedak. In Prep. Changes in mass and body condition of fasting, newly weaned southern elephant seals at Macquarie Island. ?, ??
- Blackwell, S. B., and B. J. Le Boeuf. 1993. Developmental Aspects of Sleep-Apnea in Northern Elephant Seals, Mirounga-Angustirostris. *Journal of Zoology*, 231:437-447.
- Boyd, I. L., T. A. Arnbom, and M. A. Fedak. 1994. Biomass and energy consumption of the South Georgia stock of southern elephant seals. In B. J. Le Boeuf and R. M. Laws (eds.), *Elephant Seals*, pp. 98-120. University of California Press, Los Angeles.
- Bryden, M. M. 1964. Insulating capacity of the subcutaneous fat of the southern elephant seal. *Nature*, 203:1299-1300.
- . 1972. Body size and composition of elephant seals (Mirounga leonina): absolute measurements and estimates from bone dimensions. *Journal of Zoology*, 167:265-276.
- Burnham, K. P., and D. R. Anderson. 1998. *Model Selection and Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York.
- Cahill, G. F., E. B. Marliss, and T. T. Aoki. 1979. Fat and nitrogen metabolism in fasting man. *Hormone Metab.Res.*, 2:181-185.
- Campagna, C., B. J. Le Boeuf, M. Lewis, and C. Bisioli. 1992. Equal Investment in Male and Female Offspring in Southern Elephant Seals. *Journal of Zoology*, 226:551-561.
- Carlini, A. R., M. E. I. Márquez, S. Ramdohr, H. Bornemann, H. O. Panarello, and G. A. Daneri. 2001. Postweaning Duration and Body Composition Changes in Southern Elephant Seal (Mirounga leonina) Pups at King George Island. *Physiological and Biochemical Zoology*, 74:531-540.
- Carlini, A. R., H. O. Panarello, M. E. I. Marquez, G. A. Daneri, and G. E. Soave. 2000. Energy gain and loss during lactation and postweaning in southern elephant seal pups (Mirounga leonina) at King George Island. *Polar Biol.*, 23:437-440.
- Castellini, M. A., L. D. Rea, J. L. Sanders, J. M. Castellini, and T. Zentenosavin. 1994. Developmental-Changes in Cardiorespiratory Patterns of Sleep- Associated Apnea in Northern Elephant Seals. *American Journal of Physiology-Regulatory Integrative and Comparative Physiology*, 36:R1294-R1301.

- Clutton-Brock, T. H. 1988. Reproductive success. In T. H. Clutton-Brock (ed.), *Reproductive success*, pp. 472-485. University of Chicago Press, Chicago and London.
- Croxall, J. P., T. S. McCann, P. A. Prince, and P. Rothery. 1988. Reproductive performance of seabirds and seals at South Georgia and Signy Island, South Orkney Islands, 1976-1987: Implications for Southern Ocean monitoring studies. In D. Sahrhage (ed.), *Antarctic Ocean and Resources Variability*. Springer-Verlag, Berlin.
- Drent, R. H., and S. Daan. 1980. The prudent parent: Energetic adjustments in avian breeding. *Ardea*, 68:225-252.
- Fedak, M. A., T. Arnborn, and I. L. Boyd. 1996. The relation between size of southern elephant seal mothers, the growth of their pups and the use of maternal energy, fat and protein during lactation. *Physiological Zoology*, 69:887-911.
- Field, I., M. A. Hindell, D. J. Slip, and K. J. Michael. 2001. Foraging strategies of southern elephant seals (*Mirounga leonina*) in relation to frontal zones and water masses. *Antarctic Science*, 13:371-379.
- Hindell, M. A., and M. A. Lea. 1998. Heart rate, swimming speed, and estimated oxygen consumption of a free-ranging southern elephant seal. *Physiological Zoology*, 71:74-84.
- Hindell, M. A., B. J. McConnell, M. A. Fedak, D. J. Slip, H. R. Burton, P. J. H. Reijnders, and C. R. McMahon. 1999. Environmental and physiological determinants of successful foraging by naive southern elephant seal pups during their first trip to sea. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 77:1807-1821.
- Houston, A. I., and J. M. McNamara. 1999. *Models of adaptive behaviour*. Cambridge University Press, Cambridge.
- Ihaka, R., and R. Gentleman. 1996. R: A language for data analysis and graphics. *Journal of Computational and Graphical Statistics*, 5:299-314.
- Irvine, L. G., M. A. Hindell, J. van den Hoff, and H. R. Burton. 2000. The influence of body size on dive duration of underyearling southern elephant seals (*Mirounga leonina*). *Journal of Zoology*, 251:463-471.
- Kleiber, M. 1975. *The Fire of Life: An Introduction to Animal Energetics*. R.E. Kreiger Publishing Co., Huntington, NY.
- Koenker, R. W., and G. W. Bassett. 1978. Regression quantiles. *Econometrica*, 46:33-50.
- Lebreton, J.-D., R. Pradel, and J. Clobert. 1993. The statistical analysis of survival in animal populations. *Tree*, 8:91-95.
- Ling, J. K. 1965. The skin and hair of the southern elephant seal, *Mirounga leonina* (Linn.), II. Pre-natal and early post-natal development and moulting. *Australian Journal of Zoology*, 15:349-365.
- Lunn, N. J., and I. L. Boyd. 1993a. Effects of maternal age and condition on parturition and the perinatal period of Antarctic fur seals. *Journal of Zoology*, 229:55-67.
- . 1993b. Influence of maternal characteristics and environmental variation on reproduction in Antarctic fur seals. *Symposia of the Zoological Society of London*, 66:115-129.
- McConnell, B. J., M. A. Fedak, H. R. Burton, G. H. Englehard, and P. Reijnders. 2002. Movements and foraging areas of naive, recently weaned southern elephant seal pups. *Journal of Animal Ecology*, 71:65-78.
- McCullagh, P., and J. A. Nelder. 1983. *Generalized Linear Models*. Chapman and Hall, London.
- McMahon, C. R. 2002. A demographic comparison of two elephant seal populations. PhD thesis, University of Pretoria.
- McMahon, C. R., H. Burton, S. McLean, D. Slip, and M. Bester. 2000a. Field immobilisation of southern elephant seals with intravenous tiletamine and zolazepam. *Veterinary Record*, 146:251-254.

- McMahon, C. R., H. R. Burton, and M. N. Bester. 2000b. Weaning mass and the future survival of juvenile southern elephant seals, *Mirounga leonina*, at Macquarie Island. *Antarctic Science*, 12:149-153.
- . 2003. A demographic comparison of two southern elephant seal populations. *Journal of Animal Ecology*, 72:61-74.
- Nagy, K. A., and D. P. Costa. 1980. Water flux in animals: analysis of potential errors in the tritiated water method. *Am. J. Physiol.*, 238:R454-R465.
- Noren, D. P., D. E. Crocker, T. M. Williams, and D. P. Costa. 2003. Energy reserve utilization in northern elephant seal (*Mirounga angustirostris*) pups during the postweaning fast: size does matter. *Journal of Comparative Physiology B*, DOI 10.1007/s00360-003-0353-9.
- Orsi, A. H., T. Whitworth, and W. D. Nowlin. 1995. On the Meridional Extent and Fronts of the Antarctic Circumpolar Current. *Deep-Sea Research Part I-Oceanographic Research Papers*, 42:641-673.
- Reilly, J. J., and M. A. Fedak. 1990. Measurement of the Body-Composition of Living Gray Seals By Hydrogen Isotope-Dilution. *Journal of Applied Physiology*, 69:885-891.
- Sparling, C. 2003. Causes and consequences of variation in the energy expenditure of grey seals (*Halichoerus grypus*). PhD thesis, University of St Andrews.
- Thorson, P. H., and B. J. LeBoeuf. 1994. Developmental aspects of diving in Northern elephant seal pups. In B. J. LeBoeuf and R. M. Laws (eds.), *Elephant Seals: Population Ecology, Behaviour and Physiology*, pp. 271. University of California Press, Berkeley.
- Trillmich, F. 1986. Attendance behaviour of Galapagos fur seals. In R. L. Gentry and G. L. Kooyman (eds.), *Fur seals: Maternal strategies on land and at sea*, pp. 168-185. Princeton University Press, Princeton, NJ.
- . 1996. Parental Investment in Pinnipeds. *Advanced Study of Behaviour*, 25:533-577.
- Trillmich, F., and D. Limberger. 1985. Drastic Effects of El Nino On Galapagos Pinnipeds. *Oecologia*, 67:19-22.
- Webb, P. M., D. E. Crocker, S. B. Blackwell, D. P. Costa, and B. J. Le Boeuf. 1998. Effects of buoyancy on the diving behavior of northern elephant seals. *Journal of Experimental Biology*, 201:2349-2358.
- Wheatley, K. E. 2001. Behavioural and physiological aspects of the mid-year haul-out in southern elephant seals (*Mirounga leonina*) on Macquarie Island. MSc thesis, University of St Andrews.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study*, 46:120-139.

CHAPTER 5: SUMMARY

The aim of this thesis has been to expand the current body of knowledge about reproductive strategies in polygynous pinnipeds, by examining some of the potential selective forces driving the evolution of maternal care. Rather than focusing on the variation in maternal expenditure itself, as in most previous studies, our approach was to study the consequences of this variation in terms of its effect on the offspring over the first year of nutritional independence. Although this type of information has been available for a number of large terrestrial mammals for some time, thanks to a number of excellent studies, this is the first time similar information is available for a marine mammal, or indeed, for any large marine vertebrate predator.

In this summary, I will discuss the main findings in relation to current theory as well as some of our hypotheses presented in Chapter 1. Part of this discussion will be a personal interpretation of how these results may fit within the larger context of the life history and population dynamics of this declining population. Although this interpretation is subjective, I am hoping that it will stimulate discussion about some possible directions for future research in this field.

The data presented here showed that there was a strong negative relationship between the duration of the post-weaning fast and relative departure mass, and for any given fast duration, pups with a higher weaning mass had a higher relative departure mass. The rate of mass loss decreased gradually over the fast, and although it tended to increase towards the end for long fast durations, we did not find any evidence that pups enter “Stage III fasting”, and increase their protein catabolism. One explanation for this may be the fact that we (like previous studies) found a strong positive correlation between the initial relative lipid content and the relative contribution of this lipid to the energy expenditure. It appears that the relative importance of lipid does not

vary substantially within individuals throughout the fast, but that individual pups follow different trajectories that are, in a sense, pre-determined by their onboard reserves at weaning. However, these individual patterns do not appear to be entirely determined by the initial body composition, but seemed to be modified by other individual characteristics that may require different metabolic strategies at later stages throughout the first year. For instance, while the variance in the energetic contribution of lipid was low among seals with high initial lipid contents, it increased substantially among initially leaner pups, and while lean male pups tended to adopt a slightly more protein conserving strategy, lean females appeared to be more liberal with their protein stores and conserve relatively more lipid.

As discussed in Chapter 2, differential adjustments in energy allocation, either between males and females or between lean seals, regardless of gender, may have important consequences in terms of the probability of individuals surviving their at-sea transit before they can find food. The conceptual model of time from departure to estimated starvation indicates that protein may actually be a more critical limiting resource than lipid. However, this is complicated somewhat by the fact that protein is important in terms of its absolute amount and therefore its absolute rate of depletion is critical, whereas the importance of lipid as an energy reserve and thermal insulator is related more to the relative amount. While upon reflection, a simple matching or utilization of fat and lean tissue to supplies and/or protein sparing as seen in animals that are adapted to long fasts may seem desirable, the actual situation is much more complicated. Lipid is critical for insulation; protein is important for diving and foraging ability and may have additional importance for males where large body size will later become critically important. Therefore the hormonal regulation of utilization might need a complex set of inputs that take a balance of factors into account. The best situation, not surprisingly perhaps, may be to have

a high relative lipid content surrounding a large (in absolute terms) lean body, and a similar *absolute* amount of lipid around an *absolutely* smaller lean body may, somewhat contradictory, be less favourable than a similar-sized *absolute* lean body with relatively smaller lipid reserves.

Close regulation of lipid and protein budgets while seals are fasting is clearly important. It may be equally important to regulate the lipid accumulation and body protein synthesis when seals are in a positive energy balance. The method described in Chapter 3 has great potential, and may allow us to obtain continuous measurements of the effects of these regulatory processes while animals are foraging (or fasting) at sea. For instance, if we assume that protein is a more critical limiting factor, and that seals are more severely protein depleted towards the end of the transit to feeding grounds, we may expect them to preferentially lay down protein initially after prey has been encountered. If so, it is possible that the body density to continue to increase, and the drift rates to decrease, until protein stores have been sufficiently replenished, before seals start laying down lipid reserves and drift rates to start increasing. This is an important consideration when using the drift dive method (or any other biomechanical body density estimation method) to determine the spatial distribution of feeding. An increase in body density does not automatically suggest that seals are in negative energy balance. However, the method can nevertheless provide useful information on where and when lipid assimilation occur, and an increase in relative lipid content (as indicated by decreasing body density) is still a good indication that a seal is in positive energy balance, and is likely to have replenished its protein stores as well.

The results from these studies seem to suggest that body composition is important in shaping the future patterns of growth and energetics of individual elephant seal pups during the first year of life. However, the nature of these relationships are not simple, but interact with a number of

intrinsic factors such as gender and at-sea behavioural decisions, and may also be influenced by external factors such as environmental stochasticity as well as gender and size. However, the pattern that emerges suggests that there is an important effect of size and condition on first-year survival, and that this exists in the form of a threshold. Among pups that have survived their first year, the differences in condition have been modified in such a way that initially smaller pups that are still alive have “caught up” with of their larger/better conditioned peers. In the long term, this suggests that future survival after age 1 is more strongly influenced by feeding experience, at-sea behaviour, predation and environmental variation, and less on the resources received from mothers. If these hypotheses are correct, the cost-benefit function of maternal expenditure in elephant seals may be relatively simple, in that the crucial requirement on a mother is to balance her resources in a way that balances the probability of her pup surviving its *first year* against her own future reproductive success. Any investment above this “first-year threshold” may provide the pup with a safety net, allowing it to cope with some degree of uncertainty in for instance prey availability in a given year. But the quantity of this extra insurance should only be provided within the limits defined by the marginal cost to the mother in terms of her own future performance. For a very large mother above some size/condition threshold, this cost-benefit function may reach an asymptote at some expenditure that is still small in relation to her own size/condition, and extra expenditure above this second threshold will be a “bad” investment.

In order to model these relationships, we need more information on the rate at which a mother can restore her energy reserves between breeding events, and specifically how this relates to the expenditure in the first breeding event. Some specific objectives should be:

Follow known mothers over a number of years, preferably over their entire reproductive lives.

For these mothers, we need accurate estimates of body composition, but also detailed data on

their at-sea behaviour, metabolic rate, energy expenditure and resulting change in body composition.

We will need to do further studies on the parameters that determine the shape of the first-year survival function. These parameters include 1) an upper asymptote that defines the upper boundary against the component of survival that is independent of the mother's investment, 2) a rate parameter, determining the rate at which survival increases from 0 up to this asymptote when the mother, and 3) a location parameter specifying the range of maternal investments (weaning condition) over which the highest rate of increase in survival occurs increase in survival occurs. This last parameter will essentially be determined by environmental variability (prey density and distribution). If prey availability decreases, the curve will be shifted up towards higher maternal investments. To get information on these parameters, we need to study the at-sea behaviour, energy expenditure and changes in body composition of a large number of pups while at sea. In order to account for environmental variability, this will also need to be done over a number of years.

The basis for this type of study is already in existence at Macquarie Island. Ongoing work is currently investigating the links between maternal condition and at-sea distribution and behaviour of known females over consecutive years. However, more detailed data are needed on the energy expenditure of these females, and the pup component need to be added in order to measure all the necessary parameters for the pup survival response curve and the mother's cost-benefit function. In the meantime, the data presented in this thesis may be used to develop a conceptual and theoretical model of these relationships, and to test the general response of this model to simulated variations in the important parameters. However, that is beyond the scope of this thesis.